1985

Effects of mass selection for ear length in maize

Artemio Manto Salazar
Iowa State University

INFORMATION TO USERS

This reproduction was made from a copy of a manuscript sent to us for publication and microfilming. While the most advanced technology has been used to photograph and reproduce this manuscript, the quality of the reproduction is heavily dependent upon the quality of the material submitted. Pages in any manuscript may have indistinct print. In all cases the best available copy has been filmed.

The following explanation of techniques is provided to help clarify notations which may appear on this reproduction.

1. Manuscripts may not always be complete. When it is not possible to obtain missing pages, a note appears to indicate this.

2. When copyrighted materials are removed from the manuscript, a note appears to indicate this.

3. Oversize materials (maps, drawings, and charts) are photographed by sectioning the original, beginning at the upper left hand corner and continuing from left to right in equal sections with small overlaps. Each oversize page is also filmed as one exposure and is available, for an additional charge, as a standard 35mm slide or in black and white paper format.*

4. Most photographs reproduce acceptably on positive microfilm or microfiche but lack clarity on xerographic copies made from the microfilm. For an additional charge, all photographs are available in black and white standard 35mm slide format.*

*For more information about black and white slides or enlarged paper reproductions, please contact the Dissertations Customer Services Department.

Salazar, Artemio Manto

EFFECTS OF MASS SELECTION FOR EAR LENGTH IN MAIZE

Iowa State University PH.D. 1985

PLEASE NOTE:

In all cases this material has been filmed in the best possible way from the available copy. Problems encountered with this document have been identified here with a check mark __√__.

1. Glossy photographs or pages _____
2. Colored illustrations, paper or print _____
3. Photographs with dark background _____
4. Illustrations are poor copy _____
5. Pages with black marks, not original copy _____
6. Print shows through as there is text on both sides of page _____
7. Indistinct, broken or small print on several pages _____✓_____
8. Print exceeds margin requirements _____
9. Tightly bound copy with print lost in spine _____
10. Computer printout pages with indistinct print _____
11. Page(s) _____ lacking when material received, and not available from school or author.
12. Page(s) _____ seem to be missing in numbering only as text follows.
13. Two pages numbered _____. Text follows.
14. Curling and wrinkled pages _____
15. Dissertation contains pages with print at a slant, filmed as received _____
16. Other _____

_____

_____

Effects of mass selection for ear length in maize

by

Artemio Manto Salazar

A Dissertation Submitted to the

Graduate Faculty in Partial Fulfillment of the

Requirements for the Degree of

DOCTOR OF PHILOSOPHY

Department: Agronomy
Major: Plant Breeding and Cytogenetics

Approved:

Signature was redacted for privacy.

In Charge of Major Work

Signature was redacted for privacy.

For the Major Department

Signature was redacted for privacy.

For the Graduate College

Members of the Committee:

Signature was redacted for privacy.

Iowa State University
Ames, Iowa

1985

TABLE OF CONTENTS

	Page
INTRODUCTION	1
REVIEW OF LITERATURE	3
Mass Selection in Maize	3
Indirect Selection and the Importance and Methods of Determining Genetic Properties of the Population	9
Divergent Selection Studies	11
MATERIALS AND METHODS	15
Evaluation of BSLE Subpopulations	16
Determination of Genetic Variability in BSLE Subpopulations	29
RESULTS	44
Evaluations of BSLE Subpopulations	44
Determination of Genetic Variability in BSLE Subpopulations	76
DISCUSSION	105
SUMMARY AND CONCLUSIONS	115
LITERATURE CITED	118
ACKNOWLEDGMENTS	124
APPENDIX	125

LIST OF TABLES

		Page
Table 1.	Data were recorded for the 15 traits in the indicated experiments	19
Table 2.	Analysis of variance for experiments conducted in one environment	21
Table 3.	Combined analysis of variance for the experiments conducted in different environments	22
Table 4.	Design matrices used to estimate response to selection for Eberhart's (1964) regression models	24
Table 5.	Analysis of variance used to test linear and quadratic effects for the regression models	25
Table 6.	X Matrix used to calculate genetic parameters due to changes in gene frequencies and inbreeding by selection	30
Table 7.	Analysis of variance for an individual set that includes 10 S_1 progenies of the BSLE C0, BSLE C15S, and BSLE C15L populations	31
Table 8.	Analysis of variance pooled over sets for an individual experiment	33
Table 9.	Analysis of variance pooled over sets and combined over experiments	35
Table 10.	Analysis of variance of combined experiments for the 15 traits of BSLE original and derived populations and checks which were evaluated in different environments	45
Table 11.	Combined analysis of variance for ear length and 14 other traits of BSLE original and short-ear and long-ear subpopulations of BSLE	48
Table 12.	Linear regression coefficients (units/cycle) for the 15 traits of short-ear and long-ear subpopulations of BSLE after 15 cycles of divergent mass selection for ear length	50
Table 13.	Observed means for the 15 traits of BSLE original population and after 17 cycles of divergent mass selection for ear length and two single-cross hybrid checks included in the experiments	61

Page

Table 14. Combined analysis of variance for ear length and 14 other traits of crosses between the original and short-ear and long-ear subpopulations of BSLE 64

Table 15. Linear regression coefficients (units/cycle) for the 15 traits of crosses between the original and short-ear and long-ear subpopulations of BSLE after 15 cycles of divergent mass selection for ear length 66

Table 16. Combined analysis of variance for ear length and 14 other traits of the crosses between 3SLE short-ear and long-ear subpopulations 67

Table 17. Linear regression coefficients (units/cycle) for the 15 traits of crosses between short-ear and long-ear subpopulations of BSLE after 15 cycles of divergent mass selection for ear length 69

Table 18. Combined analysis of variance for ear length and 14 other traits of BSLE populations without the check entries 70

Table 19. Genetic parameter estimates for ear length and correlated traits calculated for the original and subpopulations of BSLE selected for short and long ear length 73

Table 20. Midparent heterosis (%) of BSLE subpopulations for ear length through 15 cycles of divergent mass selection 75

Table 21. Chi-square values of the two methods for analyzing the response of BSLE subpopulations 75

Table 22. Average values ($\overline{X}$) and coefficients of variation (CV, %) for 13 traits measured in 300 S_1 lines of BSLE subpopulations evaluated in three environments 77

Table 23. Combined analysis of variance from three trials for 13 traits of 300 S_1 lines of BSLE 78

Table 24. A comparison of ear length and 12 other traits of the three BSLE subpopulations based on trials conducted in three environments 82

Table 25. Estimates of genetic variances (σ^2_G) of the three BSLE subpopulations for ear length and correlated traits based on trials conducted in three environments 83

Page

Table 26. Genetic coefficients of variability (%) of the three BSLE subpopulations for ear length and correlated traits based on trials conducted in three environments 85

Table 27. Heritabilities (%) on an individual plant basis for ear length and 12 other traits of the three BSLE subpopulations 87

Table 28. Error variances of the three BSLE subpopulations for ear length and correlated traits based on S_1 line trials conducted in three environments in Iowa 88

Table 29. Genotype by environment interaction variance estimates in three BSLE subpopulations based on S_1 line trials conducted in three environments in Iowa 89

Table 30. Genetic variance (σ^2_G) and heritabilities (h^2) on an individual plant basis for 13 traits of BSLE C0 in the three environments based on S_1 progenies 90

Table 31. Genetic correlations among 13 traits for the original BSLE population based on 100 S_1 progenies 91

Table 32. Phenotypic correlations among the traits in the original BSLE population based on 100 S_1 progenies 93

Table 33. Genetic correlations among 13 traits in cycle 15 of BSLE short-ear subpopulation based on 100 S_1 progenies 95

Table 34. Genetic correlations among 13 traits in cycle 15 of BSLE long-ear subpopulation based on 100 S_1 progenies 96

Table 35. Direct and correlated responses expected from mass selection in Iowa Long Ear Synthetic (BSLE) 98

Table 36. Efficiency of indirect selection (%) expected from mass selection in Iowa Long Ear Synthetic (BSLE) 100

Table 37. Predicted and observed response (units cycle^{-1}) after 15 cycles of mass selection for ear length in Iowa Long Ear Synthetic (BSLE) 102

Table 38. Expected response from mass selection for ear length in cycle 15 subpopulations of BSLE 103

Table A1. Analysis of variance for six agronomic traits of the original and derived subpopulations of BSLE and checks grown at Location A in Ames, Iowa, in 1982 126

Page

Table A2. Analysis of variance for ear length and 13 other traits of the original and derived populations of BSLE and checks grown at Location B in Ames, Iowa, in 1982 127

Table A3. Analysis of variance for six agronomic traits of the original and derived subpopulations of BSLE and checks grown at Ankeny, Iowa, in 1982 129

Table A4. Analysis of variance for six agronomic traits of the original and derived populations of BSLE and checks grown at Martinsburg, Iowa, in 1982 130

Table A5. Analysis of variance for six agronomic traits of the original and derived subpopulations of BSLE and checks grown at location A in Ames, Iowa, in 1983 131

Table A6. Analysis of variance for ear length and 13 other traits of original and derived populations of BSLE and checks grown at Location B in Ames, Iowa, in 1983 132

Table A7. Analysis of variance for eight agronomic traits of the original and derived subpopulations of BSLE and checks grown at Ankeny, Iowa, in 1983 134

Table A8. Observed (O) and estimated (E) ear length means (cm) with the estimated response (b) and the ratio (R) of linear regression to the total observed variation for the original and derived populations of Iowa Long Ear Synthetic 135

Table A9. Observed (O) and estimated (E) yield means (q ha^{-1}) with the estimated response (b) and the ratio (R) of linear regression to the total observed variation for the original and derived populations of Iowa Long Ear Synthetic 136

Table A10. Observed (O) and expected (E) ear diameter means (cm) with the estimated response (b) and the ratio (R) of linear regression to the total observed variation for the original and derived populations of Iowa Long Ear Synthetic 137

Table A11. Observed (O) and expected (E) cob diameter means (cm) with the estimated response (b) and the ratio (R) of linear regression to the total observed variation for the original and derived populations of Iowa Long Ear Synthetic 138

Page

Table A12. Observed (O) and expected (E) kernel depth means (cm) with the estimated response (b) and the ratio (R) of linear regression to the total observed variation for the original and derived populations of Iowa Long Ear Synthetic 139

Table A13. Observed (O) and expected (E) mean number of kernel rows with the estimated response (b) and the ratio (R) of linear regression to the total observed variation for the original and derived populations of Iowa Long Ear Synthetic 140

Table A14. Observed (O) and expected (E) ears per plant means with the estimated response (b) and the ratio (R) of linear regression to the total observed variation for the original and derived populations of Iowa Long Ear Synthetic 141

Table A15. Observed (O) and expected (E) stand count means with the estimated response (b) and the ratio (R) of linear regression to the total observed variation for the original and derived populations of Iowa Long Ear Synthetic 142

Table A16. Observed (O) and expected (E) root lodging means (%) with the estimated response (b) and the ratio (R) of linear regression to the total observed variation for the original and derived populations of Iowa Long Ear Synthetic 143

Table A17. Observed (O) and expected (E) stalk lodging means (%) with the estimated response (b) and the ratio (R) of linear regression to the total observed variation for the original and derived populations of Iowa Long Ear Synthetic 144

Table A18. Observed (O) and expected (E) means of ear droppage (%) with the estimated response (b) and the ratio (R) of linear regression to the total observed variation for the original and derived populations of Iowa Long Ear Synthetic 145

Table A19. Observed (O) and expected (E) mean grain moisture content (%) with the estimated response (b) and the ratio (R) of linear regression to the total observed variation for the original and derived populations of Iowa Long Ear Synthetic 146

Page

Table A20. Observed (O) and expected (E) mean silking date with the estimated response (b) and the ratio (R) of linear regression to the total observed variation for the original and derived populations of Iowa Long Ear Synthetic 147

Table A21. Observed (O) and expected (E) mean plant height (cm) with the estimated response (b) and the ratio (R) of linear regression to the total observed variation for the original and derived populations of Iowa Long Ear Synthetic 148

Table A22. Observed (O) and expected (R) mean ear height (cm) with the estimated response (b) and ratio (R) of linear regression to the total observed variation for the original and derived populations of Iowa Long Ear Synthetic 149

Table A23. Analysis of variance for 13 traits of 300 S_1 lines of BSLE in a test conducted at Ames, 1983 150

Table A24. Analysis of variance for 13 traits of 300 S_1 lines of BSLE in a test conducted at Ames, 1984 153

Table A25. Analysis of variance for 10 traits of 300 S_1 lines of BSLE in a test conducted at Kanawha, 1983 156

LIST OF FIGURES

		Page
Figure 1.	Direct response to divergent mass selection for ear length in Iowa Long Ear Synthetic	52
Figure 2.	Correlated response of ear diameter to divergent mass selection for ear length in Iowa Long Ear Synthetic	53
Figure 3.	Correlated response of kernel depth to divergent mass selection for ear length in Iowa Long Ear Synthetic	54
Figure 4.	Correlated response of kernel rows to divergent mass selection for ear length in Iowa Long Ear Synthetic	55
Figure 5.	Correlated response of root lodging to divergent mass selection for ear length in Iowa Long Ear Synthetic	56
Figure 6.	Correlated response of silking date to divergent mass selection for ear length in Iowa Long Ear Synthetic	57
Figure 7.	Correlated response of plant height to divergent mass selection for ear length in Iowa Long Ear Syntheitc	58
Figure 8.	Correlated response of ear height to divergent mass selection for ear length in Iowa Long Ear Synthetic	59
Figure 9.	Correlated response of grain yield to divergent mass selection for ear length in Iowa Long Ear Synthetic	60
Figure 10.	Frequency plot of 100 S_1 progenies for ear length of BSLE original (CO), short-ear (BSLE C15S), and long-ear (BSLE C15L) subpopulations	84

INTRODUCTION

Mass selection is one of the oldest and the simplest methods used in maize (Zea mays L.) improvement. It is effective for characters with high heritability. For characters with lower heritability, methods involving progeny testing among locations and years have to be used. Progeny testing, however, requires more resources, depending on the desired extent of progeny development and testing. This realization led to the idea of indirect selection. If a trait could be found that is highly correlated to an important trait that has lower heritability, it might be more efficient to work with that correlated trait rather than on the desired trait directly. In maize, ear length is one of the traits that has been found to be highly correlated with yield in some populations.

Studies involving correlated traits could help clarify the feasibility of indirect selection. These studies could also help optimize a breeding scheme by predicting the response of other traits correlated to the trait being directly selected.

Application of quantitative genetics to plant breeding has led to the formulation of equations predicting gains from different selection methods. Those formulae are functions of gene frequencies. With various cyclic population improvement schemes, gene frequencies are expected to change with selection. We cannot, however, predict such changes in gene frequencies for quantitative characters. The formulae are not valid for predicting long-term responses by use of the genetic parameters estimated for the original reference population. Hence, experiments have to be

conducted to elucidate the genetics underlying long-term selection. Except for long-term divergent selection for oil and protein content in maize, most of our knowledge of this aspect has come through studies using animals.

With the above cited considerations, a long-term divergent mass selection study for ear length in maize was initiated in 1963. The population was 'Iowa Long Ear Synthetic' (BSLE). The objectives of my study are:

1. to determine the effectiveness of mass selection for ear length;
2. to determine the response of other traits correlated with ear length through the 15 cycles of mass selection; and
3. to compare the genetic variation present in the original and the most advanced cycles (C15 short-ear and C15 long-ear) of BSLE.

REVIEW OF LITERATURE

Mass Selection in Maize

Mass selection has been effective in improving maize (Zea mays L.) populations with regard to some highly heritable traits. Mass selection in maize has been conducted for traits such as ear height, flowering time, prolificacy, leaf angle, photosynthetic efficiency, ear length, insect resistance, and yield. Effectiveness of mass selection depended on the heritability of the traits under selection, and effectiveness of mass selection has changed because of techniques used in selection.

After six years of mass selection for high and low ear placement in a maize variety, Smith (1909) derived two subpopulations with ear height of 170 and 82 cm, respectively. Vera and Crane (1970) reported positive response of 4.5 cm/cycle in a mass selection study for lower ear height after two generations at 50% selection intensity. Acosta and Crane (1972) obtained an ear height reduction of 24% in two populations after four cycles of mass selection using 50% selection intensity during the first two cycles and 20% selection intensity at the third and fourth cycles. Josephson et al. (1976) reported an ear height reduction of 3.18 cm per cycle in two synthetics after 12 generations of mass selection for lower ear height. Observed associated changes with selection for ear height reduction included reductions in plant height and yield.

Date of flowering, or silk emergence, also has been significantly altered with mass selection. Troyer and Brown (1972) selected within

late, semi-exotic synthetics for earlier silking. They reported 1.8 days reduction in flowering per cycle after six cycles of selection using a 5% selection intensity. Using mass selection within seven synthetics, Troyer and Brown (1976) obtained an average 1.7 days reduction per cycle in flowering time after five generations of selection. Correlated responses with selection for earlier silking included lower grain moisture, lower plant and ear height, and higher stalk breakage. Troyer and Brown (1976) also observed that earlier flowering increased yields among late flowering populations and decreased yields among the early ones. Hallauer and Sears (1972) reported a 20-day reduced interval between planting and silking after three cycles of mass selection in a population cross of an elite population with exotic germplasm.

Prolificacy is another trait that has been effectively handled by mass selection. Lonnquist (1967) reported the results of five generations of mass selection in 'Hays Golden' open-pollinated variety. The gain in yield by selecting for prolific type was 6.28%, which was higher than that obtained by Gardner (1961) mass selecting for yield within the same variety. Gardner (1961), using mass selection based on grain weight per plant, obtained only 3.8% gain per cycle. Torregroza and Harpstead (1967) also reported significant change in prolificacy in a divergent mass selection study after five generations. There were 28% more ears per plant and 15% greater yield in the cycle five subpopulation selected for multiple ears compared to the original population. In the single-ear selection, the number of ears per plant was reduced by 7%, and yield also was reduced by 5%. In a similar

experiment, Torregroza (1973) showed after 11 generations a 48% increase in prolificacy and 38% gain in yield for multiple-ear selection. In contrast, 16 and 7% reduction in prolificacy and yield, respectively. resulted from single-ear selection. Mass selection within a late synthetic, 'Jellicorse,' was effective for prolificacy (13.2%) and yield (33.1%) after five generations of selection for more ears per plant (Kincer and Josephson, 1976).

Genetic manipulation of leaf angle thru mass selection has also been reported. Ariyanayagam et al. (1974) conducted four cycles of bidirectional phenotypic selection for leaf angle in a variety using two leaf angle determination methods. Regression coefficients of 3.82 and 10.18 degrees per cycle were found for the two leaf angle measurements. Correlated responses with selection for more erect leaf orientation were shorter plant height, later maturity, and greater lodging resistance. Grain yield variations attributable to leaf angle differences were, however, found to be small and statistically nonsignificant at the two planting densities used.

Mass selection also was employed to change photosynthetic efficiency of some maize populations. Crosbie et al. (1981) and Crosbie and Pearce (1982) studied the effects of five cycles of recurrent phenotypic selection for higher CO_2 exchange rate (CER) in two maize populations and three cycles of low CER in one population. They obtained 1.6 and 1.3% increases in CER per cycle at the vegetative and grain filling stages, respectively, for higher CER. With selection for lower CER, a 0.7% decrease in CER at vegetative stage and a nonsignificant change for

CER at grain filling were obtained. Reduced plant and ear heights and increased resistance to root and stalk lodging were found to be correlated with selection for higher CER. Days to 50% pollen shed increased significantly with lower CER selection. Estimate of weighted average change in allelic frequency for grain yield were negative for both high and low CER selections, but the estimates were not statistically significant.

Williams and Welton (1915) concluded that ear length was mainly determined by environmental effects, therefore, selection for ear length would be ineffective. This was refuted by Sprague (1966) because ear length was shown to be a highly heritable trait. In a review of heritability studies for different traits, Hallauer and Miranda (1981) showed that ear length had an average heritability value of 38.1%, based on 36 different estimates. Preliminary results of divergent mass selection for ear length was reported by Hallauer (1968). Selection was effective in separating the original population into short-ear and long-ear subpopulations. After 10 generations, Cortez-Mendoza and Hallauer (1979) obtained significant linear changes in ear length in two subpopulations. There was a 0.32 cm (1.6%) increase and a 0.64 cm (3.2%) decrease per cycle in the long-ear and short-ear subpopulations, respectively.

In a review of studies conducted for adaptive mass selection (Lonnquist, 1967; Lonnquist and McGill, 1956; Mathema, 1971; Hallauer and Sears, 1972; Genter, 1976), Hallauer and Miranda (1981) noted that mass selection seemed to be very useful in adapting exotic or semi-exotic populations or in advancing generations of synthetic varieties

and composites. The findings of Compton et al. (1979) on the effect of mass selection on different populations with varying levels of adaptation were in agreement with the observations of Hallauer and Miranda (1981).

Zuber et al. (1971) reported significant increases in earworm resistance (Heliothis armigera Hbn.) of two maize synthetics (C and S) after 10 generations of mass selection. For synthetic C, the percentage of ears with kernel damage was reduced from 80.8% to 58.7%, an average reduction of 2.76% per generation. The percentage of ears with earworm damage for synthetic S was reduced from 64.5% to 39.2%, an average reduction of 2.81% per generation.

For characters with lower heritabilities (e.g., grain yield), the effects of mass selection have not been consistent. Gardner (1961) reviewed the early works on mass selection for yield and noted that most of them were ineffective. However, because estimates of genetic variance indicated considerable additive genetic variance for yield in most of the open-pollinated varieties (Robinson et al., 1949a; Lindsey, 1957), it was hypothesized that refinements in mass selection procedures should result in better gains. Gardner (1961) obtained an average gain of 3.9% per cycle in the first four cycles of mass selection for grain yield in the 'Hays Golden' variety. After 10 cycles, Gardner (1968) reported a linear response of grain yield of 2.7% per cycle in the control population and 4% gain per cycle in the irradiated population. After 15 generations, progress from the use of mass selection was only 0.9% gain in grain yield per year (Mareck and Gardner, 1979).

In Mexico, Johnson (1963) reported an average gain in grain yield of 11% per cycle after three cycles. Hallauer and Wright (1967) obtained an increase of 4.5% after three cycles in the open-pollinated variety 'Iowa Ideal.' Increased yield, however, was associated with an increase in grain moisture, root lodging, and dropped ears. Two additional cycles showed a nonsignificant grain yield increase (Hallauer and Sears, 1969). Eberhart et al. (1967) obtained 7.4% increase in grain yield with just one cycle of selection. Hakim et al. (1969) also reported an average of 4% gain with one cycle of selection. In a population of Nigerian composite B, Obilana (1974) obtained a 16% gain after four cycles of mass selection for grain yield.

Hallauer and Sears (1969) reported no significant yield improvement after six cycles of mass selection within the 'Krug' (BSK) maize variety. They attributed the lack of progress to mass selection in BSK to: paucity of additive genetic variance; imprecise plot techniques to minimize the confounding effects of the environment; insufficient testing to detect small differences and to estimate the true value for the different cycles of selection, particularly in the later cycles; low intensity of selection due to exclusion of stalk lodged plants in the basic unit of selection; and plant density was too high in the plots under selection. In a later study, Mulamba et al. (1983) reported a 6.9% gain after 14 cycles of mass selection or 0.49% per cycle. Increased yield was accompanied by later flowering, increased root and stalk lodging, increased grain moisture at harvest, and higher ear placement. Estimates of genetic variability based on S_1 lines showed no significant changes between cycle 0 and cycle 14 populations of BSK.

Indirect Selection and the Importance and Methods of Determining Genetic Properties of the Population

Due to the lower heritability of yield and the inconsistent effectiveness of mass selection to improve grain yield, indirect selection for a trait that is more highly heritable, but genetically correlated to yield, was suggested as a more effective breeding strategy. Some of the traits which had been used in this regard were: prolificacy (Lonnquist, 1967), photosynthetic efficiency (Crosbie and Pearce, 1982), aleurone color (Cross, 1981), and ear length (Hallauer, 1968).

Searle (1965) discussed the value of indirect selection and the ways to enhance its effectiveness. The relative efficiency of indirect selection was given as $r_g h_x/h_y$, where r_g is the genetic correlation between traits y (the basic trait) and x (the alternative trait) and h_x and h_y represent the square root of the heritabilities of traits x and y, respectively. It was concluded that indirect selection would be better than direct selection only if $r_g > h_y$, and no trait could be considered as a preferable alternative to y unless $h_x^2 > h_y^2/r_g^2$. A breeder's decision, therefore, on what selection method to use depends on his knowledge of the genetic variations and covariations in the available population.

Genetic variances in a population could be determined by the use of different mating designs, Designs I, II and III, as discussed by Cockerham (1963) and Hallauer and Miranda (1981). The latter authors also made a comprehensive survey of research that estimated the genetic variances for 19 maize traits: grain yield, plant height, ear height, ear length, number of ears, ear diameter, kernel row numbers, kernel weight, days to flower, grain moisture, oil content, lodging, number

of tillers, kernel depth, cob diameter, husk extension, husk score, flag leaf number, and flag leaf length. Most of those estimates used Designs I, II, and III, but a few were obtained by generation mean analysis of Mather (1949). It was noted that a major portion of genetic variability measured was due to additive gene effects.

Another method to estimate genetic variance is to generate unselected S_1 or more advanced lines from a test population (Wessel-Beaver et al., 1985; Tseng et al., 1984; Clucas, 1984; Martin and Russell, 1984; Mulamba et al., 1983; Lantin, 1980). In this method, it is assumed that the obtained value of genetic variance is mainly additive. Bias from nonadditive gene action could result from this assumption leading to greater expected response than the realized response. But if previous studies using more exact designs could show that nonadditive genetic effects were nonsignificant, the use of S_1 or S_2s would suffice to approximate the genetic variances of the population being evaluated.

In BSLE (Iowa Long Ear Synthetic), Hallauer (1968) estimated the genetic variances using the Design I mating plan. Hallauer (1968) reported that most of the total genetic variance for the traits measured was due to additive effects. For some characters measured, including yield and ear length, the estimates of dominance variance were negative.

With the information on the genetic variance present in a population being improved, we can compute the heritabilities for certain traits. After determining what selection method to employ and the intensity of selection, the expected genetic gain in the following cycle of selection can be computed. The expected genetic gain equation

can be represented as $\Delta G = c\sigma_p h^2 d/y$ (Falconer, 1981; Hallauer and Miranda, 1981) where ΔG = genetic gain; c = parental control; σ_p = phenotypic standard deviation; h^2 = heritability; d = selection differential; and y = number of years to complete one cycle of selection.

Divergent Selection Studies

When one or more cycles of selection have been completed, there is the problem of variability of generation means. Inspection of any graph of selection shows that the generation means fluctuate rather than proceed in a regular and smooth manner. Falconer (1981) listed some causes of such variability: random genetic drift, sampling errors in estimating generation means, differences in selection differential, and environmental factors. Drift and sampling errors could be reduced by increasing the numbers selected and measured. Differences in the selection differential could be resolved by plotting realized gain to accumulated selection differential (i.e., realized heritability). Elimination of environmental fluctuations could be done by keeping an unselected control population or a population selected in the opposite direction. The use of the latter type of control population is the one referred to as divergent selection. An early example of this type of selection in animals was the divergent selection for six-week weight in mice (Mus musculus) (Falconer, 1953). Other animals where divergent selection had been conducted include chicken (Gallus domesticus) (Benoff and Renden, 1983), quail (Coturnix coturnix japonica) (Nestor et al., 1983), mice (Hooper, 1977), cattle

(Bos taurus (Colleau et al., 1983), and fruit fly (Drosophila melanogaster) (Reeve and Robertson, 1953).

Divergent selection studies also have been conducted in sorghum (Sorghum bicolor Moench) (Ross et al., 1985), barley (Hordeum vulgare L.) (Ceccarelli and Falcinelli, 1978), tobacco (Nicotiana tabacum L.) (Beatson et al., 1984), sudangrass (Sorghum sudanense Piper) (Gorz et al., 1982), switchgrass (Panicum virgatum L.) (Vogel et al., 1981), and maize. A number of traits had been subjected to divergent selection in maize: prolificacy (Torregroza and Harpstead, 1967), earworm resistance (Zuber et al., 1971), leaf angle (Ariyanayagam et al., 1974), seed size (Padgett et al., 1968), stalk volume (Hanson, 1973), photosynthesis (Crosbie and Pearce, 1982), oil and protein (Dudley, 1977), and ear length (Cortez-Mendoza, 1977; Cortez-Mendoza and Hallauer, 1979). The majority of the divergent selection studies conducted in plants and animals reveals that asymmetrical response is more common than the exception (Falconer, 1981). Some examples will be cited.

Benoff and Renden (1983) obtained realized heritabilities of 0.49 and 0.36 for high and low 20-week body weight, respectively, in male dwarf White Leghorn chickens after three generations of selection. Nestor et al. (1983) selected for high and low 120-day egg production in quail and based on five generations reported realized heritabilities of 0.063 and 0.353, respectively. In sorghum, Ross et al. (1985) conducted four cycles of divergent mass selection for grain protein percentage; realized heritabilities were 0.10 and 0.19 for high and low strains, respectively. In barley, Ceccarelli and Falcinelli (1978)

showed that individual phenotypic selection for long and short culm resulted in asymmetrical response after four cycles with the greater response in the short direction.

Falconer (1953) listed some of the probable causes of asymmetry as follows: random drift, different selection differential for the oppositely selected lines, inbreeding depression, maternal effects, genetic asymmetry, scalar asymmetry, genes with large effects, and indirect selection. Dudley and Lambert (1969) reported the results of 65 generations of divergent selection for protein and oil content in maize. Dudley et al. (1974) stated that the asymmetry of response can be accounted for by differences in selection, changes in the selection procedures, or changes in the cultural practices. After 10 cycles of divergent mass selection for ear length, Cortez-Mendoza and Hallauer (1979) attributed the asymmetrical trend in response they obtained to genetic asymmetry. It was noted that the population used, BSLE, was synthesized from inbred lines chosen for their long ear attribute.

Falconer (1981) emphasized that some long-term selection studies showed increasing, instead of decreasing, phenotypic variance. Among the possible causes he offered were: the variance of many characters were not independent of the mean, the environmental variance may increase as the lines approach homozygozity, and the genetic variance may not decline but may even increase. Falconer (1981) cited the possible causes why the genetic variance may not decline at the apparent selection limit: the limit might not have been reached at all because completely homozygous lines might not be fit enough to survive and,

therefore, some degree of heterozygozity was needed; the limit might have been an extrinsic one imposed by the nature of the character measured; and artificial selection might have been opposed by natural selection.

MATERIALS AND METHODS

The source population used in this study was Iowa Long Ear Synthetic (BSLE). It was formed from the following 12 inbred lines selected for their long ear attribute (Russell et al., 1971):

OH29	B56
W-17R-B	N25
B217(waxy)	(Lancaster Composite)-34
N22A	C103
B55	B50
(B15xB18)-16	(L317xC.I.187-2)-1-1-9

The 12 lines were crossed to form six single crosses which were crossed to form three double crosses. All possible double-double crosses were produced from the three double crosses. Equal quantities of seed of the double-double crosses were bulked and intermated for three generations before divergent mass selection for ear length was initiated in 1963.

In the isolation field of about 16,000 plants in 1963, 100 subplots of 40 competitive plants each were designated at harvest time using the grid system of mass selection suggested by Gardner (1961). Plant density was about 40,000 plants per hectare. Within each subplot, the three shortest and three longest ears were selected for a selection intensity of 7.5%. Since 1963, two isolation plantings, one for short-ear and another for long-ear selection, have been grown each year either at Ankeny or Ames, Iowa, using the same plant density, method of selection, and selection intensity. The only restraint in the selection of ears for length was good seed set. Ears with poor seed set due to late silk emergence were not included in the short ear category.

Evaluation of BSLE Subpopulations

Field experiment

The following subpopulations and crosses were made to evaluate the trend of response after 15 cycles of mass selection for divergent ear length:

BSLE cycle 0 (C0)

BSLE short ear:	BSLE long ear:
(M-S)C3	(M-L)C3
(M-S)C6	(M-L)C6
(M-S)C9	(M-L)C9
(M-S)C12	(M-L)C12
(M-S)C15	(M-L)C15
C0 x (M-S)C3	C0 x (M-L)C3
C0 x (M-S)C6	C0 x (M-L)C6
C0 x (M-S)C9	C0 x (M-L)C9
C0 x (M-S)C12	C0 x (M-L)C12
C0 x (M-S)C15	C0 x (M-L)C15

BSLE short-ear x long-ear selection cycles:

(M-S)C3 x (M-L)C3
(M-S)C6 x (M-L)C6
(M-S)C9 x (M-L)C9
(M-S)C12 x (M-L)C12
(M-S)C15 x (M-L)C15.

Each population was increased by sib-pollinating 200 plants. Each population cross included a possible 100 plants from each population. Four checks were included in the tests: cycle 17 of short-ear and long-ear selections, (B73 x Mo17), and (B84 x Mo17).

Four experiments were conducted in 1982. Two of those were grown in separate fields at the Agronomy Research Center near Ames, one was at Ankeny, and one at Martinsburg. Three more experiments were completed in 1983: two were at Ames and the third one was at Ankeny. Experimental design was randomized complete block with three replications. Each plot

included two rows 5.5 meters long and 0.8 meter apart. The rows were overplanted using the machine planter and then thinned to 19 plants per row for an approximate plant density of 43,000 plants per hectare. All experiments were machine harvested except for two trials located at Ames, one in 1982 and another one in 1983, which were harvested by hand.

Data were collected for the following 15 traits:

1. Yield was recorded as total shelled grain weight in a plot and converted to quintals per hectare.
2. Stand count was the total number of plants available in the plot at harvest.
3. Grain moisture content (%) was measured from the shelled grain for each machine-harvested plot.
4. Ears per plant were the number of ears harvested divided by the number of plants available at harvest.
5. Ear length was the total length in cm of 10 randomly sampled ears. The total length was divided by the number of ears measured and expressed on an ear basis.
6. Ear diameter was total diameter in cm of 10 randomly sampled ears divided by the number of ears sampled.
7. Cob diameter was the total diameter in cm of 10 randomly sampled ears divided by the number of ears sampled.
8. Kernel depth was one-half the difference between the ear diameter and cob diameter and recorded in cm.

9. Number of kernel rows was the average number of kernel rows for 10 randomly sampled ears.
10. Plant height was the average height from ground level to flag leaf bearing node of five randomly sampled plants. Plant height was recorded in cm.
11. Ear height was the average height from ground level to ear bearing node of five randomly sampled plants and recorded in cm.
12. Silking date was the number of days after July 1 when 50% of the plants had visible silk.
13. Root lodging was the percentage of plants in the plot leaning 30 degrees or more from the vertical.
14. Stalk lodging was the percentage of plants in the plot broken below the top ear.
15. Dropped ears were the number of ears on the ground at harvest expressed as the percentage of the number of plants in the plot.

Not all the traits described were recorded in all the tests conducted. Table 1 includes a list of traits that data were taken at the different trials.

Statistical analysis

The statistical model used for the analysis of variance in each environment was:

$$Y_{ij} = u + R_i + P_j + e_{ij},$$

Table 1. Data were recorded for the 15 traits in the indicated experiments

Trait	Ames(A) '82	Ames(B) '82	Ankeny '82	Martins-burg '82	Ames(A) '83	Ames(B) '83	Ankeny '83
Yield	X[a]	X	X	X	X	X	X
Stand	X	X	X	X	X	X	X
Moisture	X		X	X	X		
Plant height		X				X	
Ear height		X				X	
Silking date		X				X	
Root lodging	X	X	X	X	X	X	
Stalk lodging	X	X	X	X	X	X	
Dropped ears	X	X	X	X	X		
Ear length		X				X	X
Kernel rows		X				X	X
Ear diameter		X				X	X
Cob diameter		X				X	X
Kernel depth		X				X	X
Number of ears		X				X	X

[a]Data were recorded in this experiment.

where

Y_{ij} = observed value for the jth population in the ith replication (i=1,2,3 and j=1,2,...,30);

u = overall mean effect;

R_i = effect of the ith replication;

P_j = effect of the jth population; and

e_{ij} = random error.

Replications were considered random effects while populations were considered fixed effects.

The format of the analysis of variance is shown in Table 2.

The following model was used for the combined experiments:

$$Y_{ijk} = u + E_i + R_j + P_k + (EP)_{ik} + e_{ijk},$$

where

Y_{ijk} = observed value for the kth population in the jth replication in the ith environment (i=1,2,...7; j=1,2,3; and k=1,2,...,30);

u = overall mean effect;

E_i = effect of the ith environment;

R_{ij} = effect of the jth replication in the ith environment;

P_k = effect of the kth population;

$(EP)_{ik}$ = interaction effect between the ith environment and kth population; and

e_{ijk} = random error.

Environments and replications were considered random effects while populations were considered fixed effects.

Table 2. Analysis of variance for experiments conducted in one environment

Source of variation	Degrees of freedom[a]	Mean squares	Expected mean squares
Replications	r-1		
Populations	p-1	M2	$\sigma^2 + rK_p^2$
Error	(r-1)(p-1)	M1	σ^2
Total	rp-1		

[a] r and p denote the number of replications and populations, respectively.

The form of analysis of variance for the combined experiments is shown in Table 3. Based on the expectations of mean squares, F-tests were conducted as follows:

F_E = M5/M4 for environment;

F_P = M3/M2 for population; and

F_{ExP} = M2/M1 for environment x population interaction

with the associated degrees of freedom as shown in Table 3.

Progress from mass selection for ear length was evaluated using the method proposed by Eberhart (1964). The following four models were fitted successively to partition the variation among populations and to estimate the desired genetic parameters:

$$Y_{ij} = u + B_{10}X_{oi} + d_{ij} \qquad \text{Model 1,}$$

$$Y_{ij} = u + B_{1j}X_{ij} + d_{ij} \qquad \text{Model 2,}$$

$$Y_{ij} = u + B_{1j}X_{ij} + B_{20}X_{oi}^2 + d_{ij} \qquad \text{Model 3, and}$$

$$Y_{ij} = u + B_{1j}X_{ij} + B_{2j}X_{ij}^2 + d_{ij} \qquad \text{Model 4,}$$

Table 3. Combined analysis of variance for the experiments conducted in different environments

Source of variation	Degrees of freedom[a]	Mean squares	Expected mean squares
Environments (E)	e-1	M5	$\sigma^2 + p\sigma^2_{R/E} + rp\sigma^2_E$
Replications/E	e(r-1)	M4	$\sigma^2 + p\sigma^2_{R/E}$
Populations (P)	p-1	M3	$\sigma^2 + r\sigma^2_{EP} + reK^2_P$
ExP	(e-1)(p-1)	M2	$\sigma^2 + r\sigma^2_{EP}$
Error	e(r-1)(p-1)	M1	σ^2
Total	erp-1		

[a] e, r, and p denote the number of environments, replications, and populations, respectively.

where

Y_{ij} = mean of the population in the ith cycle under jth selection direction (i=0,3,6,9,12,15 and j=1,2);

u = mean of the base population;

B_{10} = average linear regression coefficient;

B_{20} = average quadratic regression coefficient;

X_{oi},X_{ij} = design matrix coefficients;

d_{ij} = deviation from regression;

B_{ij} = linear regression coefficient for the jth selection direction; and

B_{2j} = quadratic regression coefficient for the jth selection direction.

The coefficients of the design matrices for the corresponding models are given in Table 4.

The regression coefficients were computed as follows:

b = inverse(X'X)*(X'Y),

where

b = estimate of the regression coefficient;

X = design matrix; and

Y = column vector of cycle populations.

Model 2 was used to compute the linear regression coefficient of the diverged populations.

The form of the analysis of variance to partition variation among populations to linear and quadratic effects is found in Table 5. Based on analyses in Table 5, responses to selection were tested against environment by population interaction.

The standard error (s.e.) of regression coefficient (b) was computed using the following formula (Draper and Smith, 1966):

$$s.e.(b_i) = \sqrt{\frac{c_{ii} * s^2}{r}} \quad ,$$

where

b_i = ith linear or quadratic regression coefficient;

c_{ii} = diagonal elements of the inverse (X'X) matrix, corresponding to the ith regression coefficient;

s^2 = error mean square from the analysis of variance in Table 5; and

r = number of observations used to compute an entry mean.

Table 4. Design matrices used to estimate response to selection for Eberhart's (1964) regression models

Population $Y_{i,j}$[a]	Model 1		Model 2			Model 3				Model 4				
	y	B_{10}	u	B_{11}	B_{12}	u	B_{11}	B_{12}	B_{20}	u	B_{11}	B_{12}	B_{21}	B_{22}
$Y_{0,0}$	1	0	1	0	0	1	0	0	0	1	0	0	0	0
$Y_{3,1}$	1	3	1	3	0	1	3	0	9	1	3	0	9	0
$Y_{6,1}$	1	6	1	6	0	1	6	0	36	1	6	0	36	0
$Y_{9,1}$	1	9	1	9	0	1	9	0	81	1	9	0	81	0
$Y_{12,1}$	1	12	1	12	0	1	12	0	144	1	12	0	144	0
$Y_{15,1}$	1	15	1	15	0	1	15	0	225	1	15	0	225	0
$Y_{3,2}$	1	3	1	0	3	1	0	3	9	1	0	3	0	9
$Y_{6,2}$	1	6	1	0	6	1	0	6	36	1	0	6	0	36
$Y_{9,2}$	1	9	1	0	9	1	0	9	81	1	0	9	0	81
$Y_{12,2}$	1	12	1	0	12	1	0	12	144	1	0	12	0	144
$Y_{15,2}$	1	15	1	0	15	1	0	15	225	1	0	15	0	225

[a] i could be populations *per se* or population crosses; j refers to short-ear (1) or long-ear (2) selections.

Significance of regression coefficient was tested using t-test as follows:

$$t = b_i/s.e.(b_i).$$

The calculated t was compared with tabular t at n-1 degrees of freedom, n being the number of populations being analyzed.

The modified population diallel method of Hammond and Gardner (1974) also was used to partition the variation among populations into

Table 5. Analysis of variance used to test linear and quadratic effects for the regression models

Source of variation	Degrees of freedom[a]	Sums of squares[b]	Mean squares	Expected mean squares
Environments (E)	e-1			
Replications/E	e(r-1)			
Populations (P)	p-1		M3	$\sigma^2 + r\sigma^2_{ep} + reK^2_p$
Linear	2	$re((B'X'Y)_2\text{-}CF)$	M31	$\sigma^2 + r\sigma^2_{ep} + reK^2_{p\ell}$
Average linear	1	$re((B'X'Y)_1\text{-}CF)$	M311	
Among linear	1	$re((B'X'Y)_2\text{-}(B'X'Y)_1)$	M312	
Quadratic	2	$re((B'X'Y)_4\text{-}(B'X'Y)_2)$	M32	$\sigma^2 + r\sigma^2_{ep} + reK^2_{pq}$
Average quadratic	1	$re((B'X'Y)_3\text{-}(B'X'Y)_2)$	M321	
Among quadratic	1	$re((B'X'Y)_4\text{-}(B'X'Y)_3)$	M322	
Deviations	p-5		M33	$\sigma^2 + r\sigma^2_{ep} + reK^2_{pd}$
ExP	(e-1)(p-1)		M2	$\sigma^2 + r\sigma^2_{ep}$
Error	e(r-1)(p-1)		M1	σ^2
Total	erp-1			

[a] e, r, and p denote the number of environments, replications, and populations, respectively.

[b] Subscripts indicate the model that was fit for the populations and population crosses.

components due to changes in gene frequency and inbreeding depression. An explanation of the mathematical basis of the method follows.

Assuming diploid inheritance with two alleles per locus, the mean of a random mating reference population could be derived from the following:

Genotypes	Frequencies of genotypes	Genotypic values
AA	p^2	a
Aa	2p(1-p)	d
aa	(1-p)(1-p)	-a

Population mean = (2p-1)a + 2p(1-p)d,

where

A,a = favorable and less favorables alleles, respectively;

p = frequency of the favorable allele;

a = relative value of AA genotype;

-a = relative value of aa genotype; and

d = relative value of Aa genotype.

The expression for the population mean is composed of two basic components: (2p-1)a which is attributable to homozygotes and 2p(1-p)d which is attributable to heterozygotes. These terms can be designated as A0 and 2D0, respectively. The base population mean can therefore be expressed as C0 = A0 + 2D0.

Assuming a linear change in gene frequency (Δp) through cycles of selection, the population after n cycles of selection should be:

Genotypes	Frequencies of genotypes	Genotypic values
AA	$(p+n\Delta p)^2$	a
Aa	$2(p+n\Delta p)[1-(p+n\Delta p)]$	d
aa	$[1-(p+n\Delta p)]^2$	-a

Population mean = $(2p-1)a + 2p(1-p)d + 2n\Delta pa$

$$+ 2n\Delta p(1-2p)d - 2d(n\Delta p)^2.$$

Let $\Delta pa=AL$, $\Delta p(1-2p)d=DL$ and $d\Delta p^2=DQ$, then the population mean could be expressed as: $CN = A0 + 2D0 + 2nAL + 2nDL - 2n^2DQ$.

C0 and CN have different allelic frequencies. The frequencies of A and a are p and (1-p), respectively, in C0. In CN, the frequencies of A and a are $n(p+\Delta p)$ and $n(1-p-\Delta p)$, respectively. A cross of C0 to CN would result in the following genotype frequencies:

Genotypes	Frequencies of genotypes	Genotypic values
AA	$p(p+n\Delta p)$	a
Aa	$p(1-p-n\Delta p)+(1-p)(p+n\Delta p)$	d
aa	$(1-p)(1-p-n\Delta p)$	-a

Population mean = $(2p-1)a + 2p(1-p)d + n\Delta pa + n\Delta p(1-2p)d$ or

$$C0 \times CN = \quad A0 \quad + \quad 2D0 \quad + nAL \quad + \quad nDL.$$

If from the same source population, subpopulations would be developed through different selection methods or directions, designated as I and J, then the cross of the diverged populations after n cycles of selection could be described as:

Genotypes	Frequencies of genotypes	Genotypic values
AA	$(p+ni)(p+nj)$	a
Aa	$(p+ni)(1-p-nj)+(p+nj)(1-p-ni)$	d
aa	$(1-p-ni)(1-p-nj)$	-a

In population I, frequency of A=p+ni, and in population J, frequency of A=p+nj. Population mean = (2p-1)a + 2p(1-o)d + nia + nja + ni(1-2p)d + nj(1-2p)d - $2n^2$ijd.

Let ia=ALI, ja=ALJ, i(1-2p)d=DLI, j(1-2p)d=DLJ, and ijd=H, then CIxCJ = A0 + 2D0 + nALI + nALJ + nDLI + nDLJ - $2n^2$H.

To summarize, the results of the above derivations are as follows:

C0 = A0 + 2D0;

CN = A0 + 2D0 + 2nAL + 2nDL - $2n^2$DQ;

C0xCN = A0 + 2D0 + nAL + nDL; and

CIxCJ = A0 + 2D0 + nALI + nDLI + nALJ + nDLJ - $2n^2$H.

In the above equations,

AL = partial linear regression coefficient of homozygous contribution regressed on cycles of selection;

DL = partial linear regression coefficient of heterozygous contribution regressed on cycles of selection; and

AL+DL = $n\Delta p(a+(1-2p)d) = n\Delta p\alpha$, where α is the average effect of gene substitution (Falconer, 1981). Therefore, AL+DL is the effect which could be ascribed to selection;

DQ = partial quadratic regression coefficient of heterozygous contribution regressed on cycles of selection; DQ could be interpreted as a function of inbreeding depression rather than the quadratic change in heterozygous contribution from selection (Smith, 1979a, 1979b).

H = regression of heterosis effect on the square of the difference between cycles.

The above parameters were estimated by least squares method using the matrix coefficients as indicated in Table 6. The estimated regression coefficients were tested for significance following the same procedure as what was done in Eberhart's (1964) analysis.

Determination of Genetic Variability in BSLE Subpopulations

Field experiment

From the original, cycle 15 short-ear, and cycle 15 long-ear populations, 300 S_1 lines were generated with 100 lines per population. The 300 S_1 lines were evaluated at the Agronomy Research Center near Ames and at Kanawha in 1983. Another test was conducted in 1984 at the Agronomy Research Center.

The experimental design used was a split plot in a randomized incomplete block with two replications. The 300 S_1 lines were divided into 10 sets of 30 lines each. Within each set, there were three population types with 10 lines per population type.

In all the trials, the entries were machine planted in one row plots 5.5 m long with 0.76 m between plots. The plots were overplanted and thinned to 19 plants per plot. Harvesting was done manually and the following data were recorded: yield (q ha^{-1}), stand count, number of ears, ear length (cm), ear diameter (cm), cob diameter (cm), kernel depth (cm), number of kernel rows, plant height (cm), ear height (cm), silking date, root lodging (%), and stalk lodging (%). In both of the tests at the Agronomy Research Center, data were taken on all of the traits, but at Kanawha no data were taken for silking date and lodging.

Table 6. X Matrix used to calculate genetic parameters due to changes in gene frequencies and inbreeding by selection

Population	Parameter					
	A0+2D0	AL+DL(S)	AL+DL(L)	DQ(S)	DQ(L)	H
C0	1	0	0	0	0	0
(M-S)C3	1	6	0	18	0	0
(M-S)C6	1	12	0	72	0	0
(M-S)C9	1	18	0	162	0	0
(M-S)C12	1	24	0	288	0	0
(M-S)C15	1	30	0	450	0	0
(M-L)C3	1	0	6	0	18	0
(M-L)C6	1	0	12	0	72	0
(M-L)C9	1	0	18	0	162	0
(M-L)C12	1	0	24	0	288	0
(M-L)C15	1	0	30	0	450	0
C0x(M-S)C3	1	3	0	0	0	0
C0x(M-S)C6	1	6	0	0	0	0
C0x(M-S)C9	1	9	0	0	0	0
C0x(M-S)C12	1	12	0	0	0	0
C0x(M-S)C15	1	15	0	0	0	0
C0x(M-L)C3	1	0	3	0	0	0
C0x(M-L)C6	1	0	6	0	0	0
C0x(M-L)C9	1	0	9	0	0	0
C0x(M-L)C12	1	0	12	0	0	0
C0x(M-L)C15	1	0	15	0	0	0
C3SxL	1	3	3	0	0	18
C6SxL	1	6	6	0	0	72
C9SxL	1	9	9	0	0	162
C12SxL	1	12	12	0	0	288
C15SxL	1	15	15	0	0	450

Statistical analysis

The analysis of variance for each set (Table 7) was done using the following model:

$$Y_{ijk} = u + R_i + P_k + (RP)_{ij} + (G/P)_{jk} + e_{ijk},$$

where

Table 7. Analysis of variance for an individual set that includes 10 S_1 progenies of the BSLE C0, BSLE C15S, and BSLE C15L populations

Source of variation	Degrees of freedom[a]	Mean squares	Expected mean squares
Replications (R)	r-1		
Populations (P)	p-1	M4	$\sigma_B^2 + g\sigma_A^2 + r\sigma_{E/P}^2 + rgK_P^2$
RxP (error a)	(r-1)(p-1)	M3	$\sigma_B^2 + g\sigma_A^2$
Lines/P	(g-1)p	M2	$\sigma_B^2 + r\sigma_{G/P}^2$
C0	g-1	M21	$\sigma_{B1}^2 + r\sigma_{G1}^2$
C15S	g-1	M22	$\sigma_{B2}^2 + r\sigma_{G2}^2$
C15L	g-1	M23	$\sigma_{B3}^2 + r\sigma_{G3}^2$
Error b	(r-1)(g-1)p	M1	σ_B^2
C0	(r-1)(g-1)	M11	σ_{B1}^2
C15S	(r-1)(g-1)	M12	σ_{B2}^2
C15L	(r-1)(g-1)	M13	σ_{B3}^2
Total	rpg-1		

[a] r, p, and g denote number of replications, populations, and lines within populations, respectively.

Y_{ijk} = observed value of the kth line of the jth population type in the ith replication (i=1,2; j=1,2,3; and k=1,2,...,10);

u = overall mean effect;

R_i = effect of the ith replication.

P_k = effect of the jth population;

$(RP)_{ij}$ = interaction effect of the ith replication and jth population;

$(G/P)_{jk}$ = effect of the kth line within the jth population; and

e_{ijk} = random error.

In this and the following models, population effect was considered fixed. All other effects were considered random variables.

Analyses of variance were done separately for original population (C0), cycle 15 short-ear population (C15S), and cycle 15 long-ear population (C15L) to partition the entry and error b sum of squares for each population type.

The analysis of variance, pooled over sets, for each environment (Table 8) was performed using the following model:

$$Y_{ijkm} = u + S_i + (R/S)_{ij} + (P/S)_{ik} + (RP/S)_{ijkm} + (G/P/S)_{ikm} + e_{ijk'}$$

where

Y_{ijkm} = observation for the mth line within the kth population type within the jth replication in the ith set (i=1,2,..., 10; j=1,2; k=1,2,3; and m=1,2,...,10);

u = overall mean effect;

S_i = effect of the ith set;

$(R/S)_{ij}$ = effect of the jth replication within the ith set;

$(P/S)_{ik}$ = effect of the kth population type within the ith set;

Table 8. Analysis of variance pooled over sets for an individual experiment

Source of variation	Degrees of freedom[a]	Mean squares	Expected mean squares
Sets (S)	s-1		
Replications/Sets (R/S)	(r-1)s		
Populations/Sets (P/S)	(p-1)s	M4	$\sigma_B^2 + g\sigma_A^2 + r\sigma_{G/P}^2 + rgK_P^2$
RP/S (error a)	(r-1)9p-1)s	M3	$\sigma_B^2 + g\sigma_A^2$
Lines/P/S	(g-1)ps	M2	$\sigma_B^2 + r\sigma_{G/P}^2$
C0	(g-1)s	M21	$\sigma_{B1}^2 + r\sigma_{G1}^2$
C15S	(g-1)s	M22	$\sigma_{B2}^2 + r\sigma_{G2}^2$
C15L	(g-1)s	M23	$\sigma_{B3}^2 + r\sigma_{G3}^2$
Error b	(r-1)(g-1)sp	M1	σ_B^2
C0	(r-1)(g-1)s	M11	σ_{B1}^2
C15S	(r-1)(g-1)s	M12	σ_{B2}^2
C15L	(r-1)(g-1)s	M13	σ_{B3}^2
Total	srpg-1		

[a] s, r, p, and g denote the number of sets, replications, populations, and lines, respectively.

$(RP/S)_{ijk}$ = effect of the interaction between the jth replication and the kth population type within the ith set;

$(G/P/S)_{jkm}$ = effect of the mth line within the kth population within the ith set; and

e_{ijkm} = random error.

Testing for the significance of population within set (M4) was not straightforward. An approximate F-test was calculated as follows (Satterthwaite, 1946):

$$\text{approximate } F = \frac{M4+M1}{M2+M3},$$

with

$$\text{numerator DF} = \frac{(M4+M1)^2}{\frac{(M4)^2}{DF_{M4}} + \frac{(M1)^2}{DF_{M1}}}, \text{ and}$$

$$\text{denominator DF} = \frac{(M2+M3)^2}{\frac{(M2)^2}{DF_{M2}} + \frac{(M3)^2}{DF_{M3}}},$$

where DF is the degrees of freedom and Mi are the respective mean squares. To test for the effect of lines within population within set, M2 was tested against M1.

The analysis of the combined experiments pooled over sets (Table 9) was performed using the following model:

$$Y_{ijkmn} = u + E_i + S_j + (ES)_{ij} + (R/ES)_{ijk} + (P/S)_{jm} + (EP/S)_{ijm} + (RP/ES)_{ijkm} + (G/P/S)_{jmn} + (EG/P/S)_{ijmn} + e_{ijkmn},$$

where

Y_{ijkmn} = observed value of the nth line within the mth population type within the kth replication within the jth set in the ith environment;

u = overall mean;

E_i = effect of the ith environment;

Table 9. Analysis of variance pooled over sets and combined over experiments

Source of variation	Degrees of freedom[a]	Mean squares	Expected mean squares
Environments (E)	(e-1)		
Sets (S)	(s-1)		
ExS	(e-1)(s-1)		
Replications (R)/ES	(r-1)es		
Populations (P)/S	(p-1)s	M6	$\sigma_B^2 + g\sigma_A^2 + r\sigma_{EG/P}^2 + rg\sigma_{EP}^2 + r\sigma_{G/P}^2 + regK_P^2$
ExP/S	(e-1)(p-1)s	M5	$\sigma_B^2 + g\sigma_A^2 + r\sigma_{EG/P}^2 + rg\sigma_{EP}^2$
Pooled error a	(r-1)(p-1)es	M4	$\sigma_B^2 + g\sigma_A^2$
Lines (G)/P/S	(g-1)ps	M3	$\sigma_B^2 + r\sigma_{EG}^2 + re\sigma_{G/P}^2$
C0	(g-1)s	M31	$\sigma_{B1}^2 + r\sigma_{EG1}^2 + re\sigma_{G1}^2$
C15S	(g-1)s	M32	$\sigma_{B2}^2 + r\sigma_{EG2}^2 + re\sigma_{G2}^2$
C15L	(g-1)s	M33	$\sigma_{B3}^2 + r\sigma_{EG3}^2 + re\sigma_{G3}^2$
ExG/P/S	(e-1)(g-1)ps	M2	$\sigma_B^2 + r\sigma_{EG}^2$

[a] e, s, r, p, and g denote number of environments, sets, replications, populations, and lines, respectively.

Table 9. Continued

Source of variation	Degrees of freedom	Mean squares	Expected mean squares
C0	(e-1)(g-1)s	M21	$\sigma^2_{B1} + r\sigma^2_{EG1}$
C15S	(e-1)(g-1)s	M22	$\sigma^2_{B2} + r\sigma^2_{EG2}$
C15L	(e-1)(g-1)s	M23	$\sigma^2_{B3} + r\sigma^2_{EG3}$
Pooled error b	(r-1)(g-1)esp	M1	σ^2_{B}
C0	(r-1)(g-1)es	M11	σ^2_{B1}
C15S	(r-1)(g-1)es	M12	σ^2_{B2}
C15L	(r-1)(g-1)es	M13	σ^2_{B3}
Total	esrpg-1		

S_j = effect of the jth set;

$(ES)_{ij}$ = effect of the interaction between the ith environment and jth set;

$(R/ES)_{ijk}$ = effect of the ith replication for the jth environment-kth set combination;

$(P/S)_{jm}$ = effect of the mth population type within the jth set;

$(EP/S)_{ijm}$ = effect of the interaction of the ith environment and the mth population type within the jth set;

$(RP/ES)_{ijkm}$ = effect of the interaction between the kth replication and mth population type within the ijth environment-set combination, which is error a;

$(G/P/S)_{jmn}$ = effect of the nth line within the mth population type within the jth set;

$(EG/P/S)_{ijmn}$ = effect of the interaction of the ith environment and the nth line within the mth population type within the jth set; and

e_{ijkmn} = pooled experimental error, which is error b.

Based on the expectations of mean squares shown in Table 9, Satterthwaite's approximation was employed to test for the significance of environment x population within set (M5) and population within set (M6). For M5,

approximate F = (M1+M5)/(M2+M4),

where

$$\text{numerator DF} = \frac{(M1+M5)^2}{\frac{M1^2}{DF_{M1}} + \frac{M5^2}{DF_{M5}}}, \text{ and}$$

$$\text{denominator DF} = \frac{(M2+M4)^2}{\frac{M2^2}{DF_{M2}} + \frac{M4^2}{DF_{M4}}}.$$

To test for M6, the

$$\text{approximate F} = (M2+M6)/(M3+M5),$$

where

$$\text{numerator DF} = \frac{(M2+M6)^2}{\frac{M2^2}{DF_{M2}} + \frac{M6^2}{DF_{M6}}}, \text{ and}$$

$$\text{denominator DF} = \frac{(M3+M5)^2}{\frac{M3^2}{DF_{M3}} + \frac{M5^2}{DF_{M5}}}.$$

The lines within populations within sets (M3) were tested against its interaction effect with the environment (M2). M2 was tested against error b.

Genetic variance estimates were calculated for the individual and combined experiments. Estimates of the genetic variance components for each population type were computed by equating observed mean squares to the expected mean squares. In individual experiments, the estimates of genetic variances (σ^2_G) of the three populations were calculated from Table 8 as follows:

σ^2_{G1} = (M21-M11)/r for BSLE C0;

σ^2_{G2} = (M22-M12)/r for BSLE C15S; and

σ^2_{G3} = (M23-M13)/r for BSLE C15L.

From the combined analysis (Table 9), the estimates of genetic variances and variances due to genotype by environment (σ^2_{GE}) interaction were computed as follows:

σ^2_{G1} = (M31-M21)/re for BSLE C0;

σ^2_{G2} = (M32-M22)/re for BSLE C15S;

σ^2_{G3} = (M33-M23)/re for BSLE C15L;

σ^2_{GE1} = (M21-M11)/r for BSLE C0;

σ^2_{GE2} = (M22-M12)/r for BSLE C15S; and

σ^2_{GE3} = (M23-M13)/r for BSLE C15L.

Standard errors (s.e.) for the component of variance estimates were computed by the use of the formula (Anderson and Bancroft, 1952):

$$\text{s.e. Var} = \frac{2}{c^2} \sum_k \left(\frac{MS_k^2}{DF_k+2}\right) ,$$

where

MS_k = kth mean square involved in the estimation;

DF_k = degrees of freedom associated with the kth mean square; and

c = coefficients preceding the variance components in the expectation of mean squares.

Estimates of heritability on an individual plant basis (h^2) were calculated using the estimates obtained from the analysis of combined experiments using the following formula:

$$h^2 = \sigma_G^2/(\sigma_G^2 + \sigma_{GE}^2 + 10s^2) ,$$

where

σ_G^2 = genetic variance among S_1 lines and assumed equal to the additive variance;

σ_{GE}^2 = genotype x environment interaction variance; and

s^2 = environmental variability among plots or the experimental error.

The denominator in the equation to estimate heritability is the phenotypic variance on individual plant basis. The '$10s^2$' term in the above formula was an approximation of within plant variability. Because no individual plant data were taken, this was used as an approximation of the plant-to-plant variation (Robinson et al., 1949b; Goodman, 1965; and Hallauer and Wright, 1967).

An approximation of the standard error (s.e.) for heritability estimates was obtained by the following formula (Dickerson, 1959):

$$\text{s.e. } (h^2) = (\text{s.e. } \sigma_G^2)/\sigma_P^2 ,$$

where

s.e. σ_G^2 = standard error of the genetic variance, and

σ_P^2 = phenotypic variance on individual plant basis.

Phenotypic (r_p) and genotypic (r_g) correlation coefficients were computed separately for the different populations according to the following formula (Mode and Robinson, 1959):

$$r_p = \sigma_{P_{xy}} / (\sigma^2_{P_x} * \sigma^2_{P_y})^{-\frac{1}{2}}, \text{ and}$$

$$r_g = \sigma_{G_{xy}} / (\sigma^2_{G_x} * \sigma^2_{G_y})^{-\frac{1}{2}},$$

where

$\sigma_{P_{xy}}$ = phenotypic covariance between traits x and y;

$\sigma^2_{P_x}$ = phenotypic variance of trait x;

$\sigma^2_{P_y}$ = phenotypic variance of trait y;

$\sigma_{G_{xy}}$ = genotypic covariance between traits x and y;

$\sigma^2_{G_x}$ = genotypic variance of trait x; and

$\sigma^2_{G_y}$ = genotypic variance of trait y.

Significance of the phenotypic correlations was tested using t-test as follows:

$$t = r/\sqrt{(1-r^2)/(n-2)},$$

where

n = number of entries for each pair of traits.

The computed t was compared with the tabular t at n-2 degrees of freedom.

Standard error of genotypic correlation was computed using the following formula (Mode and Robinson, 1959):

$$s.e.(r_g) = r_g\left[\frac{Vxy}{(GCxy)^2} + \frac{Vx}{4GVx} + \frac{Vy}{4GVy} - \frac{Cxyx}{GCxy(GVx)^{\frac{1}{2}}} - \frac{Cxyy}{GCxy(GVy)^{\frac{1}{2}}} + \frac{Cxyy}{2(GVx)^{\frac{1}{2}}(GVy)^{\frac{1}{2}}}\right]^{\frac{1}{2}},$$

where

$$Vxy = \frac{Vx_a * Vy_a + V^2xy_a}{DF_a+2} + \frac{Vx_b * Vy_b + V^2xy_b}{DF_b+2};$$

$$Vx = \frac{2Vx_a}{DF_a+2} + \frac{2Vx_b}{DF_b+2};$$

$$Vy = \frac{2Vy_a}{DF_a+2} + \frac{2Vy_b}{DF_b+2};$$

$$Cxyx = \frac{2Vxy_a * Vx_a}{DF_a+2} + \frac{2Vxy_b * Vx_b}{DF_b+2};$$

$$Cxyy = \frac{2Vxy_a * Vy_a}{DF_a+2} + \frac{2Vxy_b * Vy_b}{DF_b+2};$$

$$Cxy = \frac{2Vxy_a}{DF_a+2} + \frac{2Vxy_b}{DF_b+2};$$

GCxy = genetic covariance between traits x and y;

GVx = genetic variance of trait x;

GVy = genetic variance of trait y;

Vx_a, Vy_a = mean square value of lines/populations/sets (G/P/S) source of variation (M31, M32, and M33 in Table 9), with DF_a degrees of freedom, which was used in the computation of genetic variance of trait x or trait y;

Vx_b, Vy_b = mean square value of environments x lines/populations/sets (ExG/P/S) source of variation (M21, M23, and M23 in Table 9), with DF_b degrees of freedom, which was used in the computation of genetic variance of trait x or trait y;

Vxy_a = mean cross product value of G/P/S source of variation which was used in the computation of genetic covariance between traits x and y; and

Vxy_b = mean cross product value of ExG/P/S source of variation which was used in the computation of genetic covariance between traits x and y.

A genetic correlation was considered significant at 95% probability level if it was greater than twice its standard error.

Estimates of genetic gain per year (ΔG) for direct selection for trait x were calculated using the following formula (Hallauer and Miranda, 1981):

$$\Delta G = (1/2)kh^2\sigma_p;$$

where

k = 1.89 and is the standardized selection differential for 7.5% selection intensity;

h^2 = heritability on individual plant basis; and

σ_p = square root of phenotypic variance.

The predicted correlated response of trait y to direct selection for trait x was calculated as follows:

$$CR = (1/2)kh_x h_y r_g \sigma_{p_y},$$

where

k = standardized selection differential for trait x selection;

h_x = square root of the heritability of trait x;

h_y = square root of the heritability of trait y;

r_g = genetic correlation between traits x and y; and

σ_{p_y} = phenotypic standard deviation on an individual plant basis.

RESULTS

Evaluations of BSLE Subpopulations

The analysis of variance of combined experiments is presented in Table 10. There were significant differences among the populations for all the traits evaluated. Interactions of the populations with the environments, however, were not significant for all the traits. Plant height, ear height, number of kernel rows, plant stand, and percentage of dropped ears exhibited nonsignificant population by environment interaction effects. The high coefficients of variation (CV) reveal the difficulty of precisely measuring ear droppage (124.7%), root lodging (76.4%), and stalk lodging (28.6%) across environments.

There was a large range of variability in the yields obtained from the individual trials. The analysis of variance for each of the seven experiments with their respective means and coefficients of variation for the 15 traits are included in the Appendix Tables A1-A7. The highest yields were obtained in 1982 at Ames and Ankeny, which averaged 53.0 and 54.0 q ha^{-1}, respectively. The lowest yields were for Ames and Ankeny in 1983, which averaged 24.9 and 24.1 q ha^{-1}, respectively. The average yield for the 1982 trials was 43.1 q ha^{-1} compared with 29.1 q ha^{-1} for the 1983 trials. Difference in yield could be ascribed to drought conditions during the 1983 cropping season. Based on meteorological data gathered at Ames (Hallauer et al., 1982, 1983), the accumulated growing degree days from April to August were 2426.0 in 1982 and 2610.5 in 1983. The brunt of the drought came in 1983 during the month of July and the

Table 10. Analysis of variance of combined experiments for the 15 traits of BSLE original and derived populations and checks which were evaluated in different environments

Source of variation	Degrees of freedom	Mean squares					
		Ear length	Ear diameter	Cob diameter	Kernel depth	Kernel rows	Ears per plant
Environments (E)	2	190.82**	15.431**	3.377**	1.076**	37.84**	3.737**
Replications/E	6	2.77^{ns}	0.034^{ns}	0.011^{ns}	0.003^{ns}	0.35^{ns}	0.037**
Populations (P)	29	87.81**	0.231**	0.035**	0.053**	7.73**	0.038*
ExP	58	3.70**	0.051**	0.014**	0.009*	0.88^{ns}	0.023**
Error	174	1.97	0.027	0.008	0.006	0.70	
Total	269						
Mean		19.83 cm	4.26 cm	2.83 cm	0.71 cm	15.75	0.81
CV (%)		7.1	3.9	3.2	10.4	5.3	12.0

Source of variation	Degrees of freedom	Mean squares		Degrees of freedom	Mean squares	
		Yield	Stand		Root lodging	Stalk lodging
Environments (E)	6	11304.94**	5675.760**	5	6496.37**	13851.22**
Replications/E	14	102.48*	17.765*	12	238.77**	558.55**
Populations (P)	29	2026.69**	20.348*	29	407.68**	807.98**
ExP	174	84.84**	10.374^{ns}	145	131.50**	126.11**
Error	406	48.25	10.818	348	58.58	82.06
Total	629			539		
Mean		37.11 q ha^{-1}	42.9		10.02%	23.50%
CV (%)		18.7	7.7		76.4	38.6

*,** Indicate significance at 0.05 and 0.01 probability levels, respectively.

^{ns} Indicates nonsignificance.

Table 10. Continued

Source of variation	Degrees of freedom	Mean squares Dropped ears	Degrees of freedom	Mean squares Moisture	Degrees of freedom	Mean squares Silking date	Plant height	Ear height
Environments (E)	4	60.64^{ns}	3	1536.98**	1	366.94**	15661.34**	5346.45**
Replications/E	10	18.22**	8	1.60^{ns}	4	29.98**	400.87**	188.36**
Populations (P)	29	15.63**	29	3.71**	29	38.02**	3042.15*	1265.24**
ExP	116	6.53^{ns}	87	2.55*	29	5.69*	99.58^{ns}	60.36^{ns}
Error	290	6.13	232	1.86	116	3.38	107.54	57.54
Total	449		359		179			
Mean		1.98%		22.44%		31.88	242.69 cm	122.54 cm
CV (%)		124.7		6.1		5.7	4.3	6.2

early part of August, which was during the flowering and grain filling stages of the maize plant. In July 1982, total rainfall was 15.6 cm, while in July 1983 it was only 9.7 cm. Records also showed that it was much hotter during July-August in 1983 compared with 1982. The effects of the drought were so severe that I was even forced to abandon two experiments in 1983: one at Martinsburg and another (genetic variance study) at Ankeny. Generally, there was more stalk lodging than root lodging (26.2% vs. 8.6%). The worst stalk lodging occurred at Martinsburg in 1982 which could be ascribed to heavy infection by grey leaf spot (Cercospora zeae-maydis) and anthracnose (Colletotrichum gramincola) (Hallauer et al., 1982).

The analysis of variance in BSLE original and advanced populations for ear length and other traits is presented in Table 11. Except for cob diameter, ears per plant, and percentage of grain moisture, significant differences were detected among populations. Most of the variation could be ascribed to linear effect which in turn could be explained mostly by the difference in linear regressions of the diverged subpopulations. The only traits that exhibited significant quadratic effects were plant height, ear height, and plant stand. The adequacy of the linear and quadratic effects to explain variation among entries was suggested by the nonsignificant effect of deviation source of variation for all the traits.

The difference in linear response via cycles of selection for increased and reduced ear length is further demonstrated by differences in their estimated regression coefficients as shown in Table 12. Based on the regression coefficients, there were contrasting correlated

Table 11. Combined analysis of variance for ear length and 14 other traits of BSLE original and short-ear and long-ear subpopulations of BSLE

Source of variation	Degrees of freedom	Mean squares: Ear length	Ear diameter	Cob diameter	Kernel depth	Kernel rows	Ears per plant
Environments (E)	2	77.16	5.232	1.244	0.350	16.51	1.801
Replications/E	6	3.91	0.015	0.007	0.002	0.40	0.019
Populations (P)	10	158.38**	0.384**	0.026^{ns}	0.067**	12.64**	0.020^{ns}
Linear	2	779.59**	1.644**	0.045^{ns}	0.310**	58.55**	0.049^{ns}
Average lin.	1	3.29^{ns}	0.007^{ns}	0.042^{ns}	0.002^{ns}	2.99*	0.041^{ns}
Among lin.	1	1555.89**	3.281**	0.048^{ns}	0.619**	114.10**	0.058^{ns}
Quadratic	2	2.82^{ns}	0.034^{ns}	0.018^{ns}	0.001^{ns}	0.19^{ns}	0.011^{ns}
Average quad.	1	0.11^{ns}	0.002^{ns}	0.000^{ns}	0.001^{ns}	0.04^{ns}	0.012^{ns}
Among quad.	1	5.53^{ns}	0.067^{ns}	0.036^{ns}	0.001^{ns}	0.34^{ns}	0.009^{ns}
Deviation	6	3.17^{ns}	0.080^{ns}	0.022^{ns}	0.008^{ns}	1.49^{ns}	0.014^{ns}
ExP	20	2.54*	0.072**	0.015^{ns}	0.012**	0.67^{ns}	0.021*
Error	60	1.28	0.024	0.008	0.005	0.53	0.011
Total	98						

Source of variation	Degrees of freedom	Mean squares: Yield	Stand	Degrees of freedom	Mean squares: Root lodging	Stalk lodging
Environments (E)	6	3791.69	2086.16	5	2980.75	6076.84
Replications/E	14	39.69	13.33	12	66.35	214.58
Populations (P)	10	548.89**	25.31*	10	595.78**	894.55**
Linear	2	2372.72**	48.63*	2	2473.95**	4178.24**
Average lin.	1	2909.51**	0.41^{ns}	1	50.05^{ns}	2327.47**
Among lin.	1	1895.33**	96.85**	1	4897.85**	6029.00**

*,**Indicate significance at 0.05 and 0.01 probability levels, respectively.

^{ns}Indicates nonsignificance.

Table 11. Continued

Source of variation	Degrees of freedom	Mean squares: Yield	Mean squares: Stand	Degrees of freedom	Mean squares: Root lodging	Mean squares: Stalk lodging
Quadratic	2	91.19^{ns}	38.41*	2	238.57^{ns}	70.82^{ns}
Average quad.	1	171.50^{ns}	15.60^{ns}	1	39.86^{ns}	103.22^{ns}
Among quad.	1	10.87^{ns}	61.22*	1	437.28^{ns}	38.42^{ns}
Deviation	6	93.52^{ns}	13.17^{ns}	6	88.79^{ns}	74.56^{ns}
ExP	60	77.58*	10.18^{ns}	50	198.49**	161.00**
Error	140	54.34	9.35	120	63.34	100.39
Total	230			197		

Source of variation	Degrees of freedom	Mean squares: Dropped ears	Degrees of freedom	Mean squares: Grain moisture	Degrees of freedom	Mean squares: Silking date	Mean squares: Plant height	Mean squares: Ear height
Environments (E)	4	7.86	3	651.77	1	196.91	5472.74	1845.47
Replications/E	10	9.58	8	1.80	4	14.40	264.11	85.12
Populations (P)	10	17.40**	10	4.22^{ns}	10	58.54**	4982.23**	2294.89**
Linear	2	76.48**	2	12.64*	2	260.03**	23586.00**	10848.85**
Average lin.	1	11.93^{ns}	1	22.44*	1	1.55^{ns}	265.80^{ns}	82.98^{ns}
Among lin.	1	141.02**	1	2.83^{ns}	1	518.52**	46906.20**	21614.70**
Quadratic	2	4.54^{ns}	2	3.69^{ns}	2	13.19^{ns}	697.64*	396.69*
Average quad.	1	0.62^{ns}	1	0.35^{ns}	1	7.17^{ns}	73.02^{ns}	172.67^{ns}
Among quad.	1	8.46^{ns}	1	7.02^{ns}	1	19.21^{ns}	1322.26**	620.71*
Deviation	6	1.99^{ns}	6	1.59^{ns}	6	6.49^{ns}	209.17^{ns}	76.30^{ns}
ExP	40	4.73^{ns}	30	2.13^{ns}	10	5.74^{ns}	112.08^{ns}	75.87^{ns}
Error	400	6.07	80	1.46	40	4.96	148.47	52.30
Total	164		131		65			

Table 12. Linear regression coefficients (units/cycle) for the 15 traits of short-ear and long-ear subpopulations of BSLE after 15 cycles of divergent mass selection for ear length

Traits	BSLE subpopulations	
	Short-ear	Long-ear
Ear length, cm	-0.46 ±0.03**	0.38 ±0.03**
Yield, q ha^{-1}	-1.04 ±0.11**	-0.44 ±0.11**
Ear diameter, cm	0.021±0.004**	-0.017±0.004**
Cob diameter, cm	0.007±0.002*	0.002±0.002^{ns}
Kernel depth, cm	0.007±0.002*	-0.009±0.002**
Kernel rows, no.	0.15 ±0.02**	-0.08 ±0.02**
Ears $plant^{-1}$	-0.007±0.002*	-0.002±0.002^{ns}
Stand, no.	0.08 ±0.05^{ns}	-0.06 ±0.05^{ns}
Root lodging, %	-0.63 ±0.13**	0.42 ±0.13*
Stalk lodging, %	-1.30 ±0.17**	-0.13 ±0.17^{ns}
Dropped ears, %	-0.15 ±0.04*	0.04 ±0.04^{ns}
Moisture, %	0.07 ±0.02*	0.10 ±0.02**
Silking date, no.	-0.26 ±0.06**	0.33 ±0.06**
Plant height, cm	-3.23 ±0.35**	2.39 ±0.35**
Ear height, cm	-2.14 ±0.21**	1.67 ±0.21**

*,** Indicate significance at 0.05 and 0.01 probability levels, respectively.

^{ns} Indicates nonsignificance.

changes for the agronomic traits between the two subpopulations. Compared to the long-ear selection, the short-ear subpopulation was characterized as having larger ear diameter, deeper kernels, more kernel rows, less root lodging, earlier silking, and shorter plant and ear heights. Both subpopulations, however, showed a significant

decrease in yield. The observed and predicted linear responses to divergent mass selection for ear length in BSLE are depicted in Figures 1 to 9.

The differences in the rates of response for the two selection directions also are evident in Table 12. In the primary trait selected (ear length), the rate of change per cycle was greater with short-ear subpopulation compared with the long-ear subpopulation: -0.46 vs. 0.38 cm per cycle. Differential responses also occurred for other traits (Table 12). Correlated responses with selection for ear length were asymmetrical for yield (-1.04 for short-ear vs. -0.44 q ha^{-1} $cycle^{-1}$ for long-ear), number of kernel rows (0.15 for short-ear vs. -0.08 rows $cycle^{-1}$ for long-ear), root lodging (-0.63 for short-ear vs. 0.42% $cycle^{-1}$ for long-ear), plant height (-3.23 for short-ear vs. 2.39 cm $cycle^{-1}$ for long-ear), and ear height (-2.14 for short-ear vs. 1.67 cm $cycle^{-1}$ for long-ear).

Complete listing of observed means and predicted values based on linear regression analysis for the 15 traits of the advanced cycles tested are included in Appendix Tables A8-A22. Other comparisons of interest are the observed means for the original BSLE population and the checks, which are presented in Table 13. Average ear length of the original BSLE (BSLE C0) population was similar to that of the single-cross hybrid checks. BSLE C0 and the single-cross hybrids also were similar for plant height, ear height, grain moisture, and plant stand. Compared to the single-cross hybrid checks, however, BSLE C0 yielded almost 50% less. BSLE C0 also had shallower kernels,

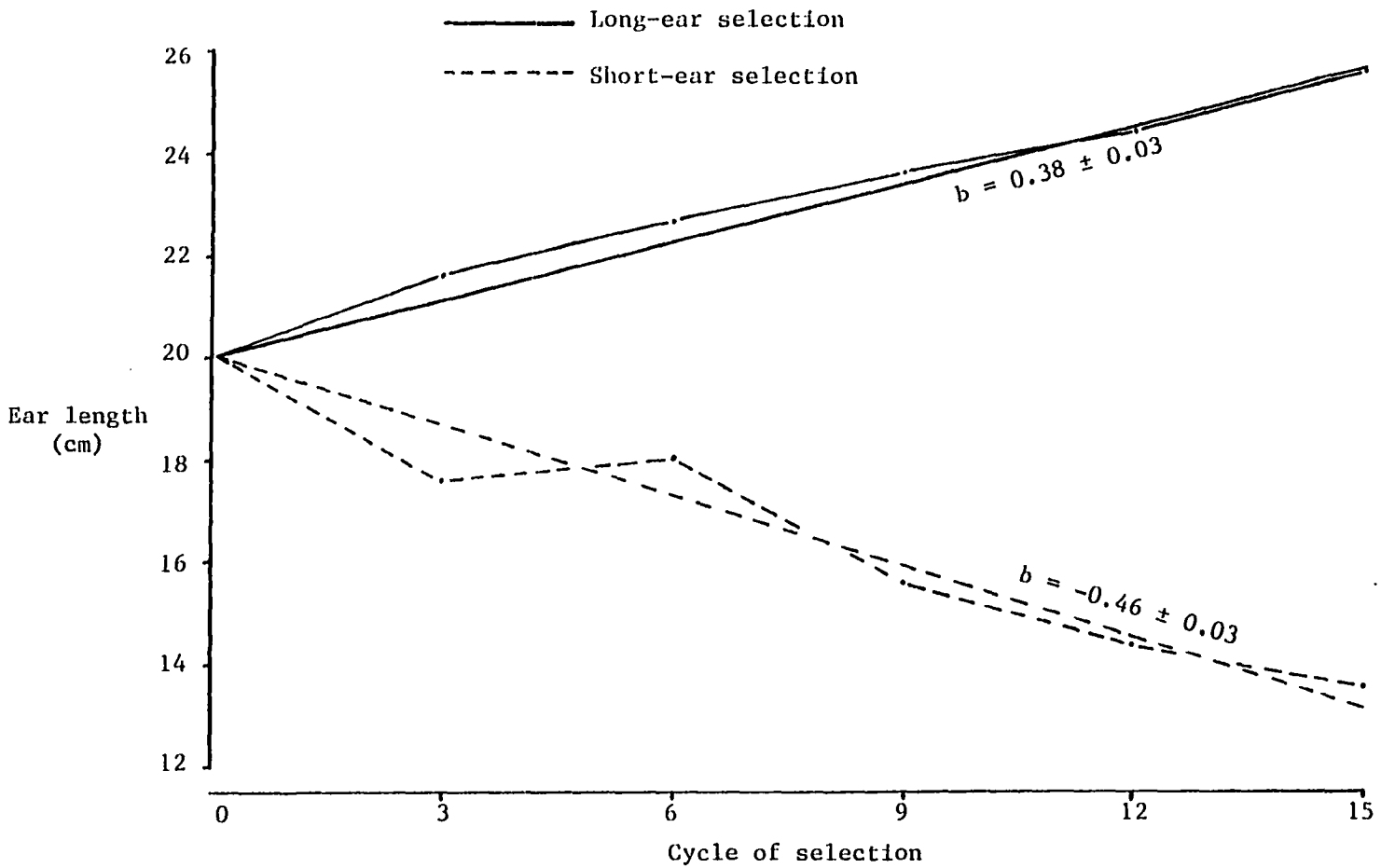

Figure 1. Direct response to divergent mass selection for ear length in Iowa Long Ear Synthetic

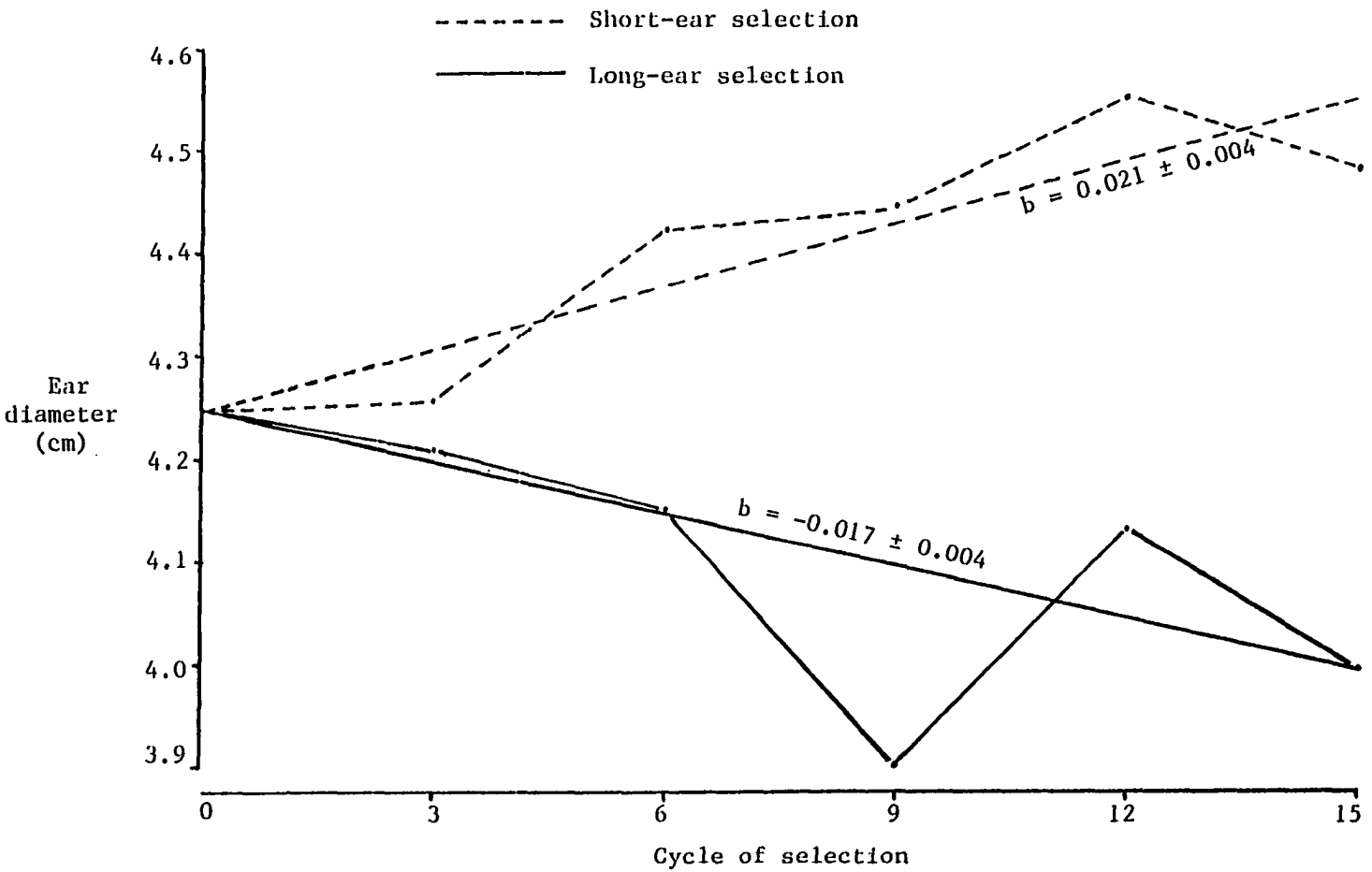

Figure 2. Correlated response of ear diameter to divergent mass selection for ear length in Iowa Long Ear Synthetic

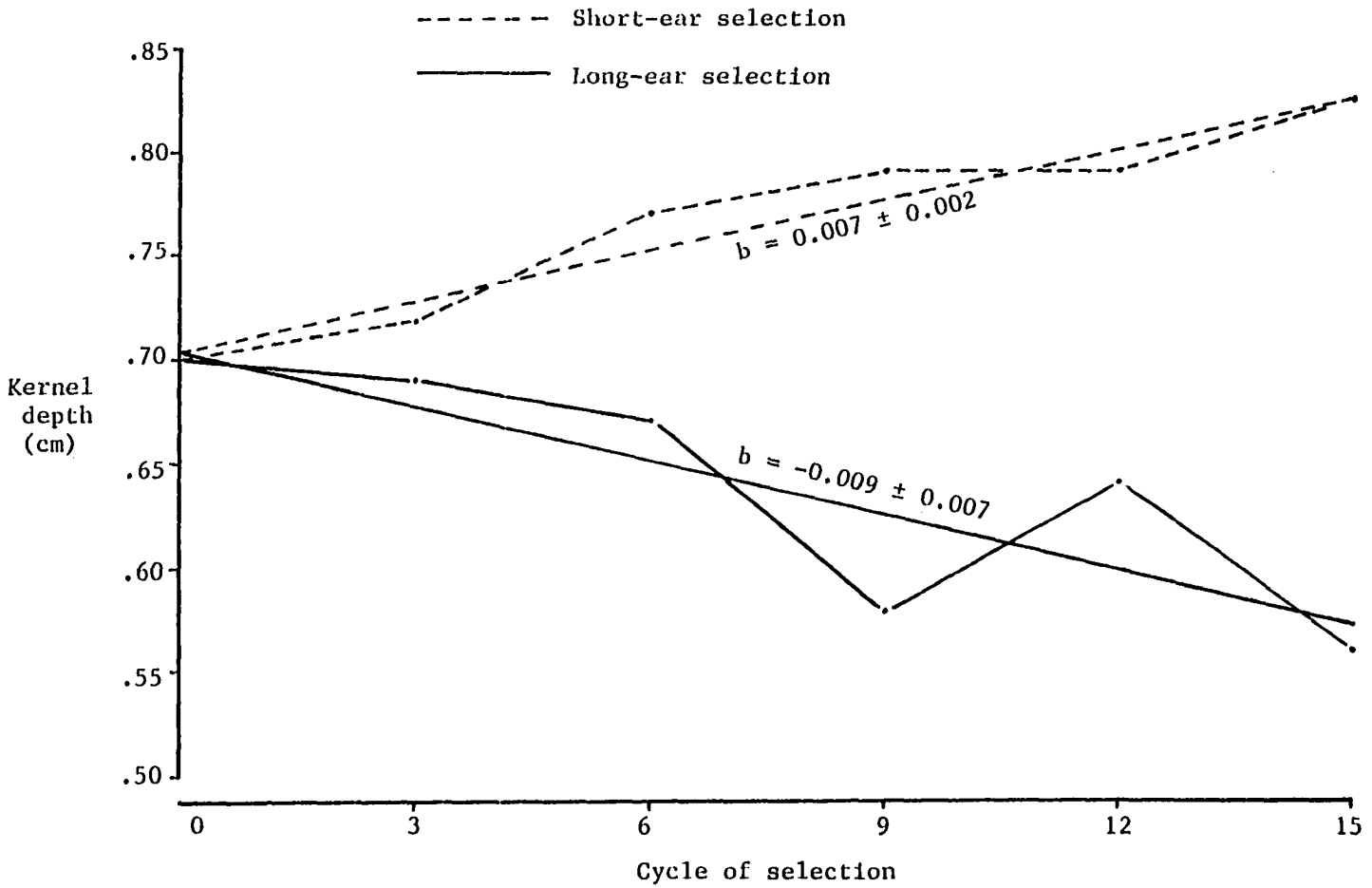

Figure 3. Correlated response of kernel depth to divergent mass selection for ear length in Iowa Long Ear Synthetic

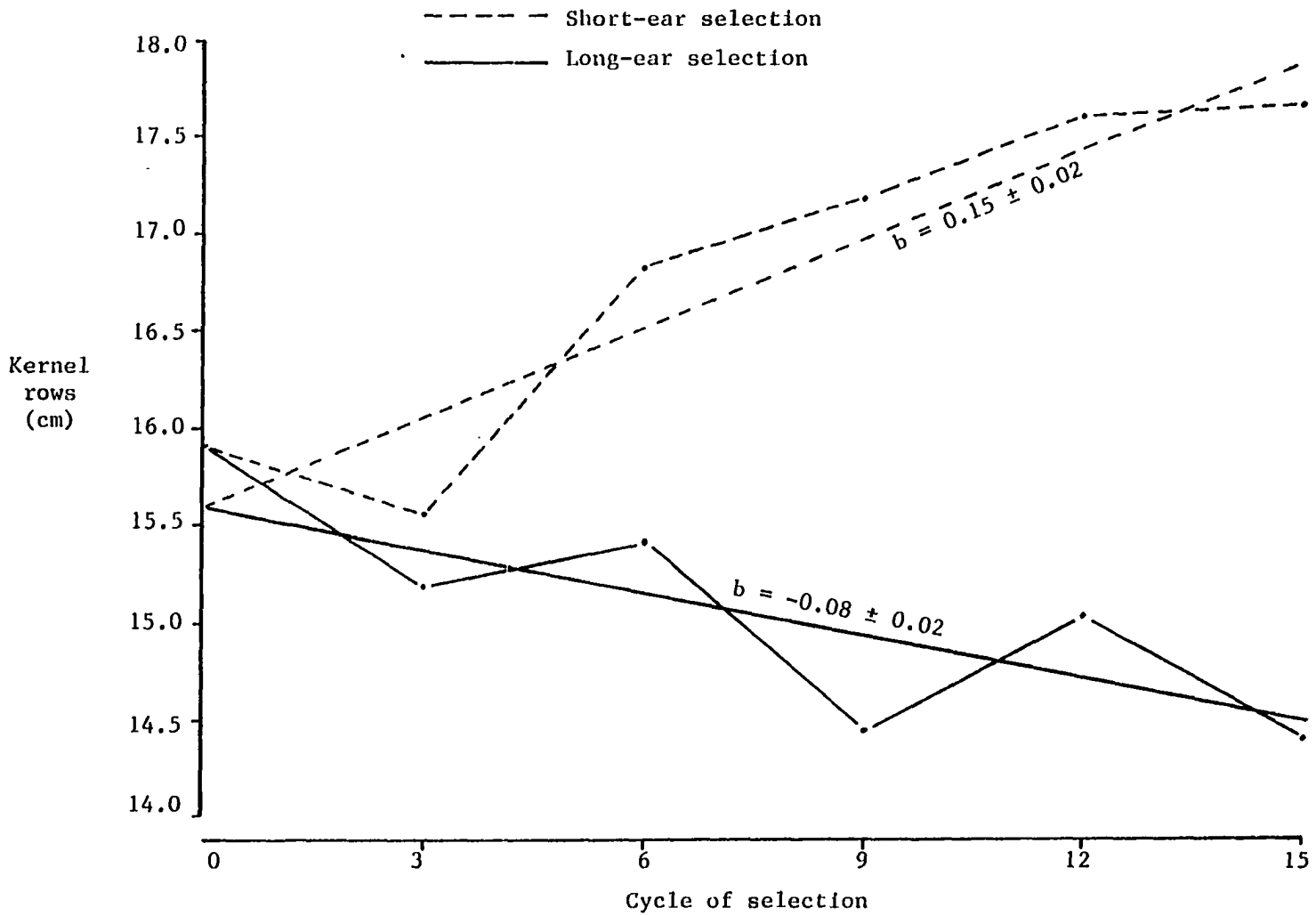

Figure 4. Correlated response of kernel rows to divergent mass selection for ear length in Iowa Long Ear Synthetic

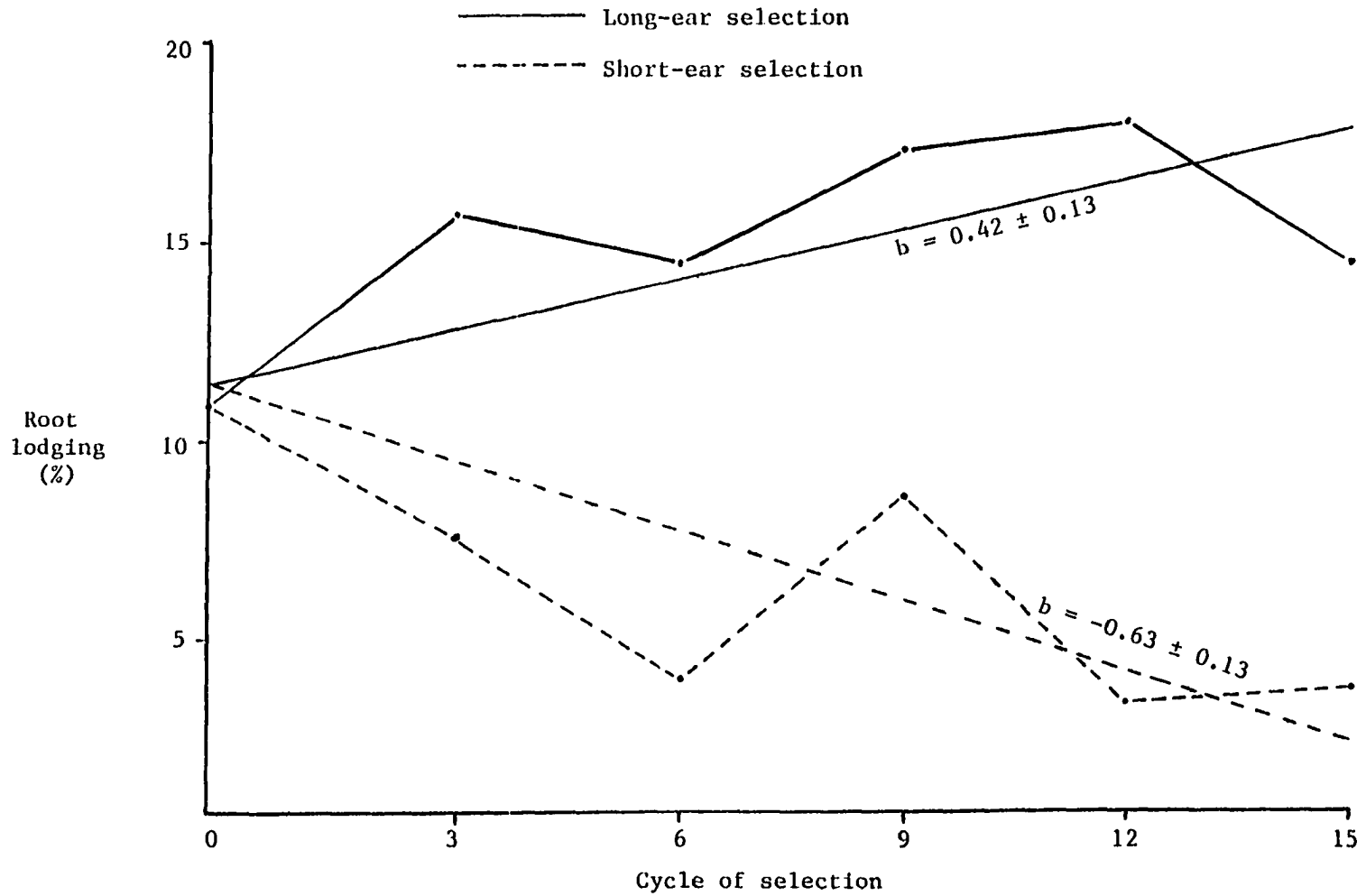

Figure 5. Correlated response of root lodging to divergent mass selection for ear length in Iowa Long Ear Synthetic

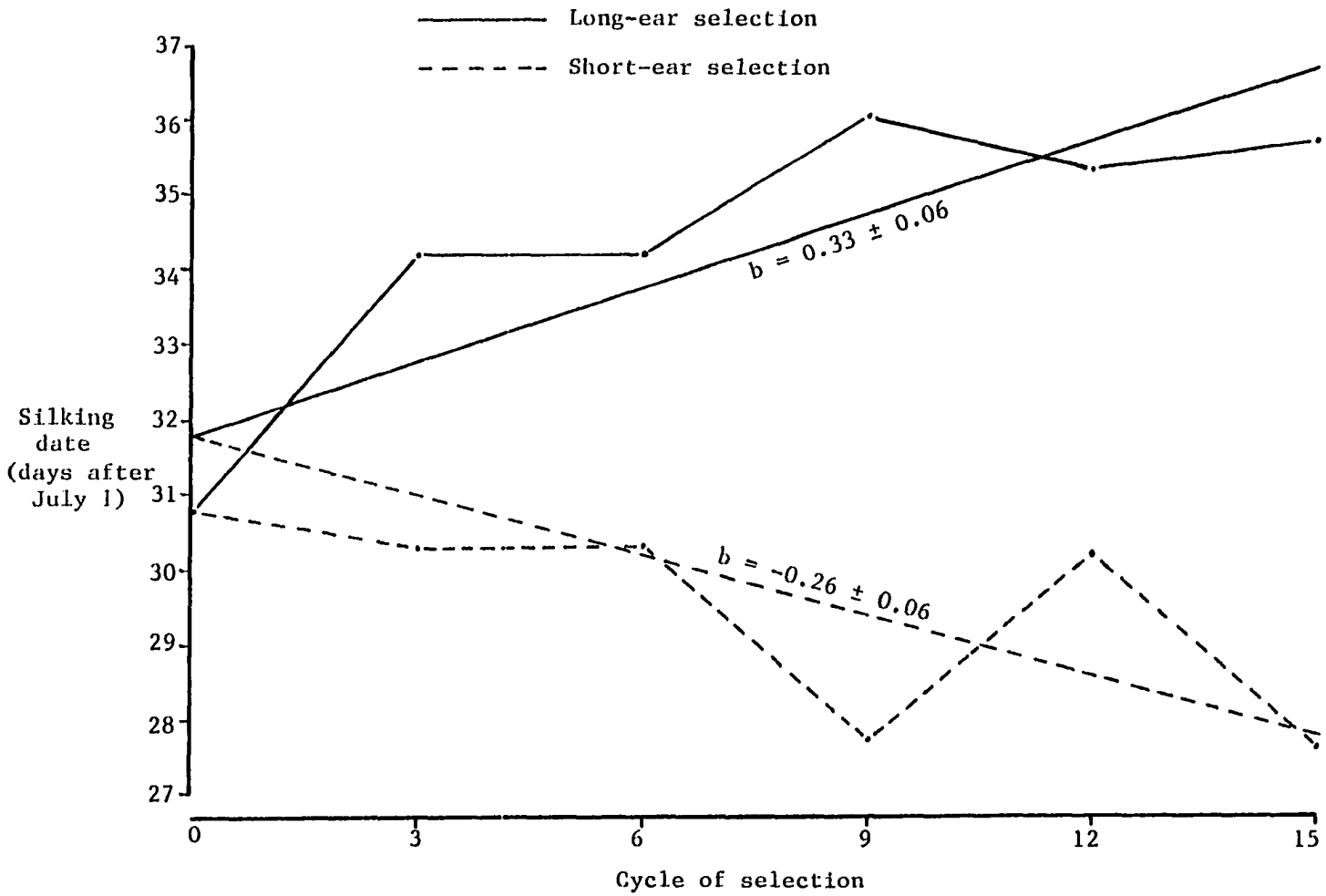

Figure 6. Correlated response of silking date to divergent mass selection for ear length in Iowa Long Ear Synthetic

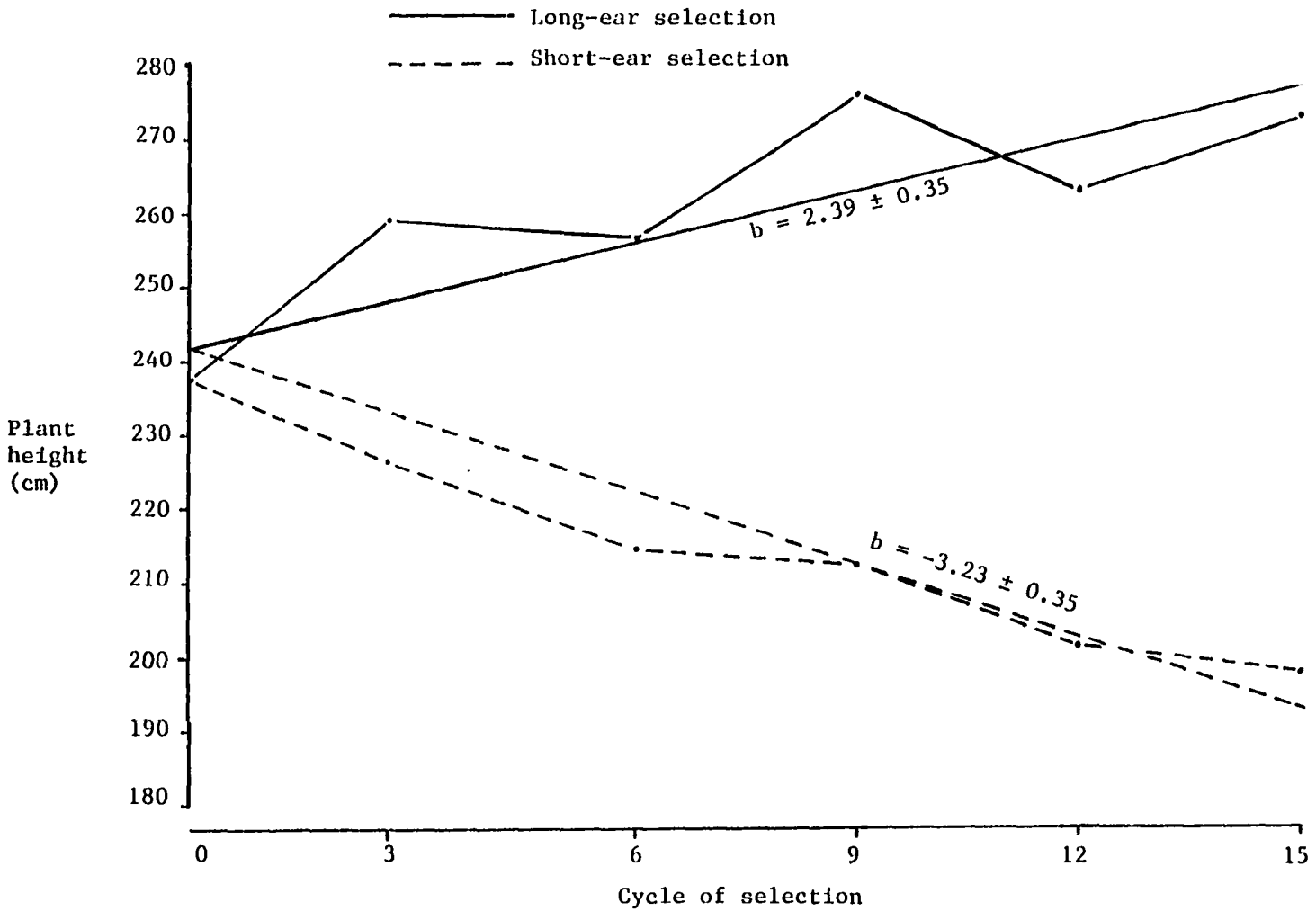

Figure 7. Correlated response of plant height to divergent mass selection for ear length in Iowa Long Ear Synthetic

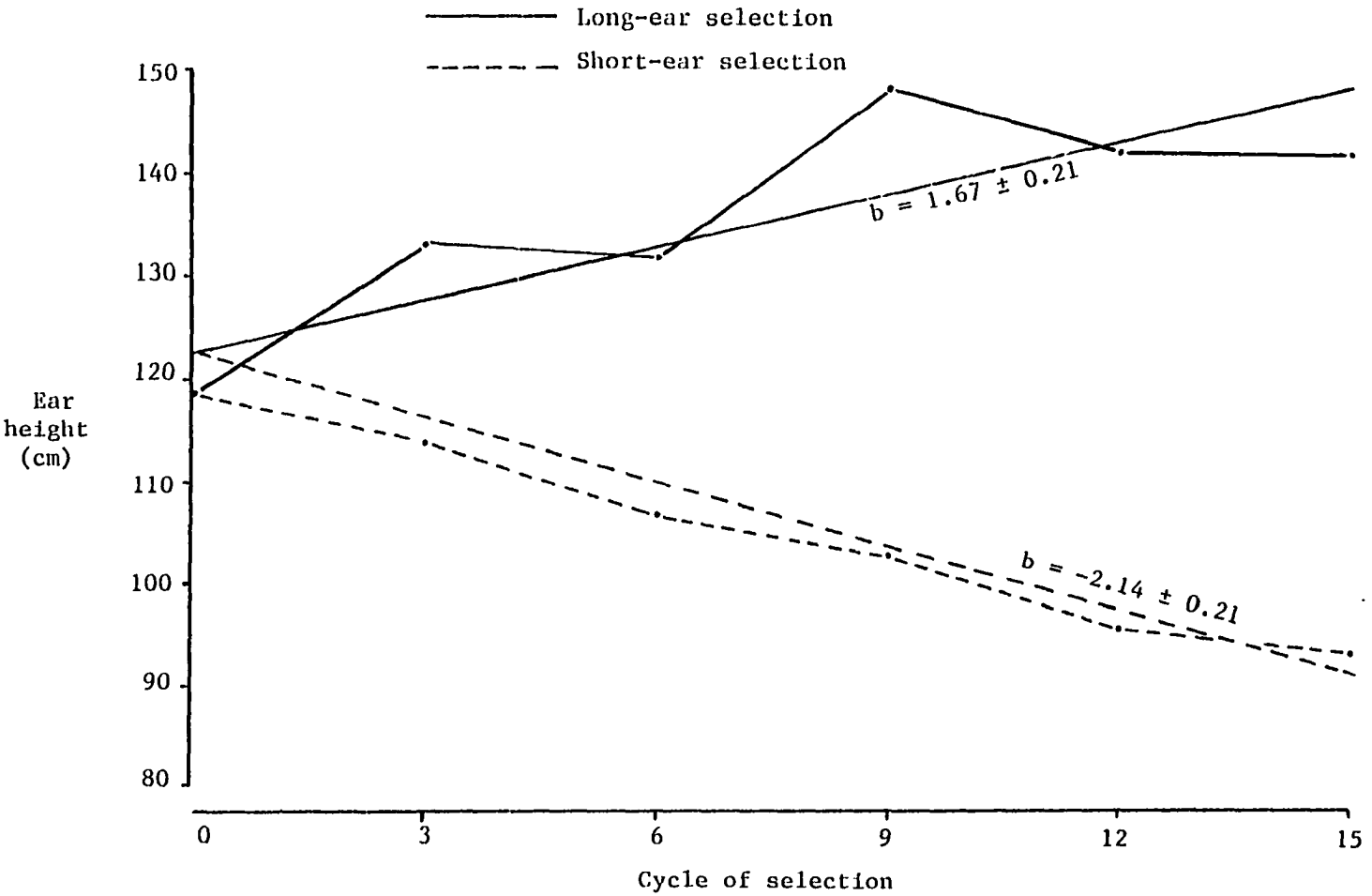

Figure 8. Correlated response of ear height to divergent mass selection for ear length in Iowa Long Ear Synthetic

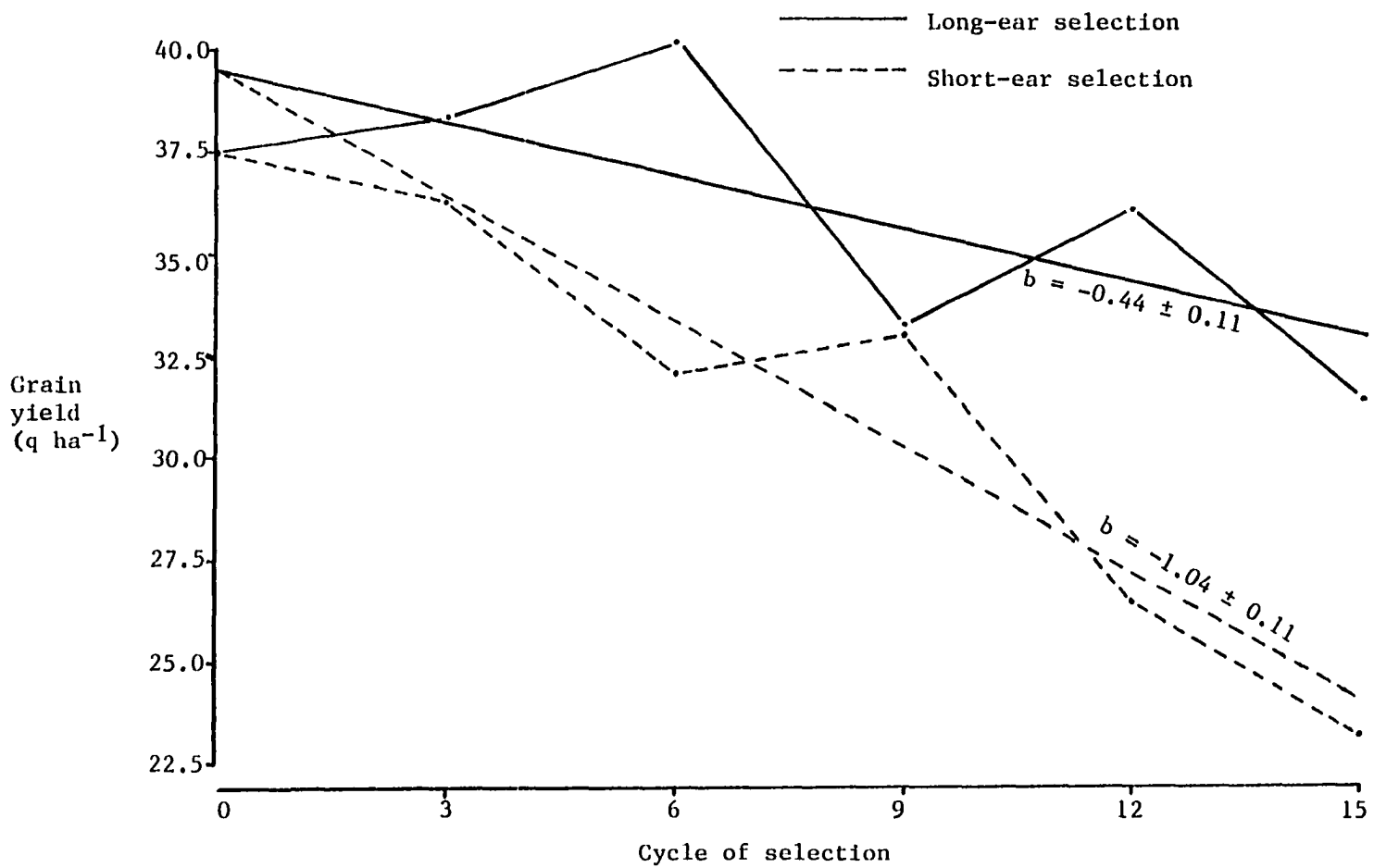

Figure 9. Correlated response of grain yield to divergent mass selection for ear length in Iowa Long Ear Synthetic

Table 13. Observed means for the 15 traits of BSLE original population and after 17 cycles of divergent mass selection for ear length and two single-cross hybrid checks included in the experiments

Entry[a]	Yield	Ear length	Ear diameter	Cob diameter	Kernel depth	Plant height	Ear height
	q ha^{-1}	cm					
BSLE C0	37.5	20.02	4.23	2.81	0.71	238.0	118.8
BSLE C17S	24.3	12.96	4.37	2.84	0.76	197.0	91.8
BSLE C17L	32.4	25.04	3.93	2.76	0.59	271.5	137.7
B73 x Mo17	73.7	19.80	4.47	2.70	0.88	239.0	121.0
B84 x Mo17	66.0	19.57	4.41	2.63	0.86	237.3	121.7
LSD (0.05)	4.2	1.30	0.15	0.08	0.07	11.9	8.7

[a]BSLE C0 is the original, unselected population of BSLE; C17S is BSLE after 17 cycles of mass selection for shorter ear length; C17L is BSLE after 17 cycles of mass selection for increased ear length; and B73 x Mo17 and B84 x Mo17 are elite single-cross hybrids.

[b]Number of days after July 1 when 50% of the plants had visible silk.

Root lodging	Stalk lodging	Dropped ears	Moisture	Kernel rows	Ears per plant	Stand	Silking date[b]
		%			no.		
10.7	32.3	2.36	22.0	15.9	0.79	43.0	30.8
1.5	10.0	0.14	22.5	17.8	0.75	42.0	29.0
15.1	28.2	2.41	23.7	14.7	0.84	41.1	36.3
5.4	11.7	0.14	21.6	15.2	1.00	44.2	26.7
9.3	8.7	1.08	21.8	15.5	1.01	40.8	28.5
5.0	5.9	1.78	1.1	0.8	0.09	2.0	2.1

greater lodging and ear droppage, and later silking time. After 17 cycles of mass selection, BSLE C0 had diverged in the directions recorded in Table 13.

Information on the change in general combining ability of the subpopulation can be obtained by examining the data on crosses between the original and advanced cycles of BSLE. The analysis of variance of the crosses is shown in Table 14. Significant variation was detected for ear length and the correlated traits kernel depth, kernel-row number, root and stalk lodging, silking time, plant height, and ear height. Most of the variation was explained by linear effects. The nature of the significant linear effects can be analyzed by examining the regression coefficients of the population crosses that are presented in Table 15. For long-ear subpopulation by BSLE C0 crosses, only ear length and plant and ear heights had significant regression coefficients. There were more significant regression coefficients in the crosses between BSLE C0 and short-ear subpopulations. Therefore, it seems that for most of the traits correlated with ear length, the difference in general combining ability between the short-ear and long-ear subpopulations was due to greater changes in the short-ear subpopulations than in the long-ear subpopulations.

The data on crosses between short-ear and long-ear subpopulations can be used to determine whether genetic divergence had developed between the two subpopulations for the expression of heterosis. The analysis of variance for the subpopulation crosses is presented in Table 16. It is apparent from Table 16 that there were few significant changes for

Table 14. Combined analysis of variance for ear length and 14 other traits of crosses between the original and short-ear and long-ear subpopulations of BSLE

Source of variation	Degrees of freedom	Mean squares: Ear length	Ear diameter	Cob diameter	Kernel depth	Kernel rows	Ears per plant
Environments (E)	2	71.61**	5.568**	1.548**	0.306**	14.69**	1.480**
Replications/E	6	3.28	0.021	0.011	0.003	0.31	0.014
Populations (P)	10	26.41**	0.081^{ns}	0.009^{ns}	0.018**	3.20**	0.005^{ns}
Linear	2	118.74**	0.372**	0.006^{ns}	0.075**	11.71**	0.010^{ns}
Average lin.	1	0.96^{ns}	0.009^{ns}	0.000^{ns}	0.003^{ns}	0.52^{ns}	0.000^{ns}
Among lin.	1	236.52**	0.735**	0.009^{ns}	0.114**	22.91**	0.020^{ns}
Quadratic	2	1.81^{ns}	0.012^{ns}	0.015^{ns}	0.009^{ns}	1.08^{ns}	0.001^{ns}
Average quad.	1	3.58^{ns}	0.018^{ns}	0.009^{ns}	0.012^{ns}	2.12^{ns}	0.000^{ns}
Among lin.	1	0.04^{ns}	0.003^{ns}	0.021^{ns}	0.009^{ns}	1.84^{ns}	0.000^{ns}
Deviation	6	3.84^{ns}	0.012^{ns}	0.009^{ns}	0.003^{ns}	1.06^{ns}	0.005^{ns}
ExP	20	4.48*	0.036*	0.012^{ns}	0.006^{ns}	0.54^{ns}	0.007^{ns}
Error	60	2.35	0.020	0.008	0.004	0.72	0.010
Total	98						

Source of variation	Degrees of freedom	Mean squares: Yield	Stand	Degrees of freedom	Mean squares: Root lodging	Stalk lodging
Environments (E)	6	4910.52**	2101.27**	5	2574.11**	6104.42**
Replications/E	14	73.72	17.06	12	250.82	383.96
Populations (P)	10	27.84^{ns}	10.88^{ns}	10	289.90**	277.78*
Linear	2	67.39^{ns}	12.72^{ns}	2	1256.70**	701.21**
Average lin.	1	43.73^{ns}	12.34^{ns}	1	34.77^{ns}	673.08*
Among lin.	1	89.85^{ns}	13.11^{ns}	1	2478.62**	729.33*

*,** Indicate significance at 0.05 and 0.01 probability levels, respectively.

^{ns} Indicates nonsignificance.

Table 14. Continued

Source of variation	Degrees of freedom	Mean squares: Yield	Mean squares: Stand	Degrees of freedom	Mean squares: Root lodging	Mean squares: Stalk lodging
Quadratic	2	7.95^{ns}	12.70^{ns}	2	22.84^{ns}	313.42^{ns}
Average quad.	1	0.10^{ns}	21.79^{ns}	1	20.63^{ns}	588.39*
Among quad.	1	15.81^{ns}	3.61^{ns}	1	25.04^{ns}	38.44^{ns}
Deviation	6	21.48^{ns}	9.65^{ns}	6	56.66^{ns}	124.76^{ns}
ExP	60	51.53^{ns}	9.73^{ns}	50	102.40**	102.89^{ns}
Error	140	50.99	12.91	120	57.74	84.27
Total	230			197		

Source of variation	Degrees of freedom	Mean squares: Dropped ears	Degrees of freedom	Mean squares: Grain moisture	Degrees of freedom	Mean squares: Silking date	Mean squares: Plant height	Mean squares: Ear height
Environments (E)	4	60.53**	3	544.24**	1	136.74*	7339.64**	2257.52*
Replications/E	10	10.41	8	1.19	4	11.67	105.94	227.33
Populations (P)	10	2.17^{ns}	10	1.66^{ns}	10	9.07*	1667.78**	581.51**
Linear	2	2.60^{ns}	2	0.42^{ns}	2	30.95**	7125.07**	2513.27**
Average lin.	1	3.73^{ns}	1	0.45^{ns}	1	0.09^{ns}	192.39^{ns}	24.29^{ns}
Among lin.	1	1.47^{ns}	1	0.38^{ns}	1	61.82**	14057.75**	5002.26**
Quadratic	2	1.19^{ns}	2	0.92^{ns}	2	12.85*	419.18*	120.95^{ns}
Average quad.	1	0.00^{ns}	1	1.42^{ns}	1	21.49*	780.18*	194.67^{ns}
Among quad.	1	2.38^{ns}	1	0.42^{ns}	1	4.21^{ns}	88.19^{ns}	47.24^{ns}
Deviation	6	2.35^{ns}	6	2.31^{ns}	6	0.52^{ns}	264.88^{ns}	91.10^{ns}
ExP	40	4.47^{ns}	30	2.68^{ns}	10	2.48^{ns}	83.67^{ns}	47.72^{ns}
Error	100	8.02	80	1.94	40	2.40	99.91	49.97
Total	164		131		65			

Table 15. Linear regression coefficients (units/cycle) for the 15 traits of crosses between the original and short-ear and long-ear subpopulations of BSLE after 15 cycles of divergent mass selection for ear length

Traits	Crosses	
	C0 x short ear	C0 x long ear
Ear length, cm	-0.18 ±0.04**	0.14 ±0.04**
Yield, q ha^{-1}	-0.16 ±0.11^{ns}	-0.02 ±0.11^{ns}
Ear diameter, cm	0.011±0.003*	-0.007±0.003^{ns}
Cob diameter, cm	0.001±0.002^{ns}	-0.001±0.002^{ns}
Kernel depth, cm	0.005±0.001**	-0.003±0.001^{ns}
Kernel rows	0.06 ±0.02*	-0.04 ±0.02^{ns}
Ears per plant	-0.002±0.002^{ns}	0.001±0.002^{ns}
Stand	0.07 ±0.06^{ns}	0.02 ±0.06^{ns}
Root lodging, %	-0.46 ±0.13**	0.28 ±0.13^{ns}
Stalk lodging, %	-0.59 ±0.15**	-0.18 ±0.15^{ns}
Dropped ears, %	0.02 ±0.05^{ns}	0.04 ±0.05^{ns}
Moisture, %	0.01 ±0.03^{ns}	0.02 ±0.03^{ns}
Silking date, days	-0.11 ±0.04*	0.09 ±0.04^{ns}
Plant height, cm	-1.89 ±0.29**	1.18 ±0.29**
Ear height, cm	-1.04 ±0.20**	0.79 ±0.20**

*,**Indicate significance at 0.05 and 0.01 probability levels, respectively.

^{ns}Indicates nonsignificance.

the crosses between the diverged subpopulations of BSLE for the different cycles of selection. The only significant effect was obtained with stalk lodging. These trends were confirmed by the regression coefficients which also showed nonsignificance for all the traits except stalk lodging (Table 17).

Table 16. Combined analysis of variance for ear length and 14 other traits of the crosses between BSLE short-ear and long-ear subpopulations

Source of variation	Degrees of freedom	Mean squares: Ear length	Ear diameter	Cob diameter	Kernel depth	Kernel rows	Ears per plant
Environments (E)	2	20.38*	3.546**	0.610**	0.297**	10.10**	0.665**
Replications/E	6	3.60	0.046	0.005	0.010	0.17	0.025
Populations (P)	5	2.46^{ns}	0.040^{ns}	0.014^{ns}	0.004^{ns}	1.25^{ns}	0.005^{ns}
Linear	1	4.29^{ns}	0.004^{ns}	0.018^{ns}	0.000^{ns}	0.00^{ns}	0.001^{ns}
Deviation	4	2.00^{ns}	0.049^{ns}	0.013^{ns}	0.005^{ns}	1.56^{ns}	0.006^{ns}
ExP	10	3.63^{ns}	0.024^{ns}	0.008^{ns}	0.005^{ns}	0.71^{ns}	0.012*
Error	30	2.23	0.042	0.012	0.005	0.72	0.005
Total	53						

Source of variation	Degrees of freedom	Mean squares: Yield	Stand	Degrees of freedom	Mean squares: Root lodging	Stalk lodging
Environments (E)	6	2806.04**	1152.50**	5	689.44**	3958.48**
Replications/E	14	75.07	9.66	12	117.35	128.15
Populations (P)	5	53.27^{ns}	0.53^{ns}	5	44.03^{ns}	453.71**
Linear	1	163.76*	1.20^{ns}	1	172.70^{ns}	1383.41**
Deviation	4	25.65^{ns}	0.36^{ns}	4	11.86^{ns}	221.28*
ExP	30	28.82^{ns}	11.20^{ns}	25	47.92^{ns}	79.37^{ns}
Error	70	44.04	9.92	60	50.90	86.98
Total	125			107		

*,**Indicate significance at 0.05 and 0.01 probability levels, respectively.

^{ns}Indicates nonsignificance.

Table 16. Continued

Source of variation	Degrees of freedom	Mean squares: Dropped ears	Degrees of freedom	Mean squares: Grain moisture	Degrees of freedom	Mean squares: Silking date	Mean squares: Plant height	Mean squares: Ear height
Environments (E)	4	40.38**	3	305.72**	1	51.36*	1965.44^{ns}	850.69*
Replications/E	10	2.92	8	2.12	4	4.39	370.44	97.94
Populations (P)	5	13.39^{ns}	5	1.48^{ns}	5	6.38^{ns}	257.38^{ns}	94.29^{ns}
Linear	1	18.62^{ns}	1	4.55^{ns}	1	0.29^{ns}	95.24^{ns}	21.49^{ns}
Deviation	4	12.08^{ns}	4	0.71^{ns}	4	7.90^{ns}	297.92^{ns}	112.49^{ns}
ExP	20	11.37^{ns}	15	3.27^{ns}	5	3.09^{ns}	111.38^{ns}	24.16^{ns}
Error	50	7.71	40	1.82	20	2.82	118.84	90.11
Total	89		71		35			

Table 17. Linear regression coefficients (units/cycle) for the 15 traits of crosses between short-ear and long-ear subpopulations of BSLE after 15 cycles of divergent mass selection for ear length

Traits	Regression coefficients
Ear length, cm	0.06 ± 0.04^{ns}
Yield, q ha^{-1}	-0.02 ± 0.12^{ns}
Ear diameter, cm	0.002 ± 0.005^{ns}
Cob diameter, cm	0.004 ± 0.003^{ns}
Kernel depth, cm	-0.001 ± 0.002^{ns}
Kernel rows	-0.0004 ± 0.0225^{ns}
Ears per plant	-0.001 ± 0.002^{ns}
Stand	-0.02 ± 0.05^{ns}
Root lodging, %	-0.25 ± 0.13^{ns}
Stalk lodging, %	$-0.70 \pm 0.18^{*}$
Dropped ears, %	-0.09 ± 0.06^{ns}
Moisture, %	0.05 ± 0.03^{ns}
Silking date, days	-0.02 ± 0.05^{ns}
Plant height, cm	-0.32 ± 0.35^{ns}
Ear height, cm	-0.15 ± 0.31^{ns}

*Indicates significance at 0.05 probability level.

^{ns}Indicates nonsignificance.

From the use of the modified population diallel analysis of Hammond and Gardner (1974), changes in the two subpopulations (BSLE short-ear and long ear) could be evaluated in terms of allelic frequency changes and inbreeding. From the nature of the entries used in this study, existence of heterosis could also be tested. The analysis of variance for the BSLE subpopulations without the checks is included in Table 18.

Table 18. Combined analysis of variance for ear length and 14 other traits of BSLE populations without the check entries

Source of variation	Degrees of freedom	Mean squares					
		Ear length	Ear diameter	Cob diameter	Kernel depth	Kernel rows	Ears per plant
Environments (E)	2	163.44**	13.271**	3.161**	0.877**	35.70**	3.744**
Replications/E	6	3.43	0.040	0.012	0.004	0.33	0.036
Populations (P)	25	74.98**	0.201**	0.017^{ns}	0.036**	6.91**	0.011^{ns}
ExP	50	3.66**	0.049**	0.013*	0.008**	0.65^{ns}	0.014^{ns}
Error	150	2.09	0.025	0.009	0.005	0.64	0.009
Total	233						

Source of variation	Degrees of freedom	Mean squares		Degrees of freedom	Mean squares	
		Yield	Stand		Root lodging	Stalk lodging
Environments (E)	6	10262.67**	4939.08**	5	5942.88**	13969.37**
Replications/E	14	80.42	15.98	12	249.95	539.98
Populations (P)	25	296.00**	14.90^{ns}	25	384.29**	498.28**
ExP	150	61.11**	10.56^{ns}	125	137.29**	112.01*
Error	350	48.88	10.89	300	57.42	86.50
Total	545			467		

*,** Indicate significance at 0.05 and 0.01 probability levels, respectively.

^{ns} Indicates nonsignificance.

Table 18. Continued

Source of variation	Degrees of freedom	Mean squares Dropped ears	Degrees of freedom	Mean squares Grain moisture	Degrees of freedom	Mean squares Silking date	Mean squares Plant height	Mean squares Ear height
Environments (E)	4	66.98*	3	1358.62**	1	351.00**	14868.78**	4829.64**
Replications/E	10	15.82	8	1.40	4	25.23	382.56	176.36
Populations (P)	25	13.06*	25	3.02^{ns}	25	27.62**	2815.98**	1182.73**
ExP	100	6.67*	75	2.43*	25	4.19^{ns}	91.60^{ns}	53.35^{ns}
Error	250	6.66	200	1.78	100	3.45	110.21	60.58
Total	389		311		155			

Significant variation was detected among entries for all the traits except ears per plant, cob diameter, stand, and grain moisture. There were significant variations for all the traits when the single-cross hybrids were included (Table 10).

The AL+DL term accounts for gene frequency changes due to selection, DQ estimates inbreeding depression, and H estimates heterosis. The estimates from the analysis that include these terms are presented in Table 19. The AL+DL term was significant for ear length in both subpopulations. For yield and other correlated traits (cob diameter, ears per plant, dropped ears, and moisture), however, the AL+DL terms were not significant for both subpopulations. DQ was not significant for most of the traits with the exception of yield for BSLE short-ear and plant height for BSLE long-ear subpopulations. H was nonsignificant for all the correlated traits, but it was significant for ear length, which was the primary trait of selection.

Midparent heterosis estimates for ear length through 15 cycles of divergent mass selection are presented in Table 20. Heterosis decreased from cycle 3 to cycle 6, increased at cycle 6, and increased for cycles 12 and 15.

A chi-square goodness-of-fit test was conducted to compare the predictions based on the two methods of analysis used in this study. The results of these tests are shown in Table 21. The results of the analysis based on the linear model suggested by Eberhart (1964) were neither better nor inferior than the gene frequency analysis based on Hammond and Gardner's (1974) model. It was observed, however, from

Table 19. Genetic parameter estimates for ear length and correlated traits calculated for the original and subpopulations of BSLE selected for short and long ear length

Traits	CO	AL+DL	
		Short ear	Long ear
Ear length	20.09±0.25**	-0.207±0.031**	0.155±0.031**
Yield	37.92±0.79**	-0.155±0.099^{ns}	-0.005±0.099^{ns}
Ear diameter	4.22±0.027**	0.013±0.003**	-0.002±0.000^{ns}
Cob diameter	2.83±0.02**	0.003±0.002^{ns}	-0.001±0.002^{ns}
Kernel depth	0.69±0.01**	0.005±0.001**	-0.003±0.001^{ns}
Kernel rows	15.37±0.14**	0.084±0.017**	-0.023±0.017^{ns}
Ears per plant	0.81±0.02**	-0.003±0.002^{ns}	0.001±0.002^{ns}
Stand	42.52±0.38**	0.111±0.047*	0.016±0.047^{ns}
Root lodging	11.42±0.93**	-0.455±0.115**	0.368±0.115**
Stalk lodging	29.06±1.14**	-0.565±0.142**	-0.091±0.142**
Dropped ears	2.25±0.35**	-0.013±0.043^{ns}	0.040±0.043^{ns}
Moisture	22.08±0.20**	0.018±0.025^{ns}	0.012±0.025^{ns}
Silking days	32.32±0.40**	-0.148±0.049**	0.117±0.049*
Plant height	249.10±2.23**	-1.992±0.277**	1.394±0.277**
Ear height	125.41±1.66**	-1.107±0.205**	0.989±0.205**

[a]Values still exist but beyond the third decimal digit and were rounded to zero.

*,**Indicate significance at 0.05 and 0.01 probability levels, respectively.

[ns]Indicates nonsignificance.

DQ		
Short ear	Long ear	H
-0.002 ± 0.002^{ns}	0.002 ± 0.002^{ns}	$0.004\pm0.002^{*}$
$-0.021\pm0.006^{**}$	-0.012 ± 0.006^{ns}	-0.001 ± 0.005^{ns}
-0.002 ± 0.000^{ns}	0.000^{a}	0.000
0.000	0.000	0.000
0.000	0.000	0.000
0.000	0.000	0.000
0.000	0.000	0.000
-0.005 ± 0.003^{ns}	-0.002 ± 0.003^{ns}	-0.004 ± 0.003^{ns}
0.012 ± 0.007^{ns}	-0.014 ± 0.007^{ns}	-0.009 ± 0.006^{ns}
-0.002 ± 0.009^{ns}	0.006 ± 0.009^{ns}	0.005 ± 0.008^{ns}
-0.005 ± 0.003^{ns}	-0.002 ± 0.003^{ns}	-0.002 ± 0.002^{ns}
0.001 ± 0.002^{ns}	0.003 ± 0.002^{ns}	0.001 ± 0.001^{ns}
0.000	0.001 ± 0.003^{ns}	0.001 ± 0.003^{ns}
0.009 ± 0.018^{ns}	$-0.094\pm0.018^{*}$	0.001 ± 0.015^{ns}
-0.003 ± 0.013^{ns}	-0.024 ± 0.013^{ns}	-0.008 ± 0.011^{ns}

Table 20. Midparent heterosis[a] (%) of BSLE subpopulations for ear length through 15 cycles of divergent mass selection

Cycle	Midparent heterosis
3	3.25
6	0.36
9	1.47
12	4.46
15	9.02

[a] $H = \left(\frac{F_1 - MP}{MP}\right) \times 100$, where H = midparent heterosis; F_1 = cross of corresponding advanced cycles of BSLE short-ear and long-ear subpopulations; and MP = mean value for the parents used to generate the F_1.

Table 21. Chi-square values of the two methods[a] for analyzing the response of BSLE subpopulations

Traits	Advanced cycles		Crosses of original to advanced cycles		Crosses of advanced cycles	
	Linear	GFA	Linear	GFA	Linear	GFA
Ear length	0.150	0.191	0.147	0.164	0.040	0.029
Yield	1.032	0.850	0.187	0.214	0.140	0.131
Ear diameter	0.015	0.014	0.002	0.004	0.005	0.007
Cob diameter	0.006	0.006	0.003	0.003	0.002	0.002
Kernel depth	0.009	0.009	0.006	0.007	0.003	0.005
Kernel rows	0.066	0.078	0.061	0.071	0.040	0.064
Ears per plant	0.014	0.014	0.004	0.005	0.003	0.003
Stand	0.171	0.142	0.092	0.106	0.002	0.010
Root lodging	6.872	5.165	2.767	3.317	0.312	0.828
Stalk lodging	1.857	1.979	2.802	2.889	2.087	2.853
Dropped ears	-0.907	0.201	0.510	0.685	1.046	5.415
Moisture	0.062	0.050	0.059	0.063	0.010	0.012
Silking days	0.347	0.395	0.149	0.194	0.163	0.169
Plant height	1.777	2.224	1.613	1.744	0.807	0.856
Ear height	1.582	1.584	1.033	1.168	0.609	0.554

[a] Linear - by fitting simple linear regression (Eberhart, 1964); GFA - gene frequency analysis (Hammond and Gardner, 1974).

the gene frequency analysis for ear length of the crosses of advanced cycles that smaller chi-square values were obtained. This suggests that the response to selection for ear length of the crosses of advanced cycles could be better described by invoking selection and heterotic effects rather than by only the linear analysis of the plot of observed points.

Determination of Genetic Variability in BSLE Subpopulations

The means and coefficients of variation of the 13 traits measured in S_1 lines of the three BSLE subpopulations are presented in Table 22. The yield obtained in 1984 was better than in 1983 which can be ascribed to the heat and drought conditions experienced in 1983. Higher coefficients of variation also were obtained for yield in 1983 compared with 1984. Minimal root lodging occurred in the 1984 test compared with the 1983 tests (0.5% vs. 15.1%). Stalk lodging, however, was greater in 1984 than in 1983 (18.4% vs. 12.4%).

The analyses of variance combined for environments are presented in Table 23. Significant variations were observed among the subpopulations for all the traits except plant stand and root lodging. The performance of the S_1 lines within each subpopulation also differed significantly except for lodging traits and plant stand in BSLE C0 and lodging traits in BSLE cycle 15 short-ear (BSLE C15S) subpopulation. Interaction of the subpopulations with the environments was significant for all traits except plant stand, ears per plant, and stalk lodging.

Table 22. Average values ($\bar{X}$) and coefficients of variation (CV, %) for 13 traits measured in 300 S_1 lines of BSLE subpopulations evaluated in three environments

Traits	Environments							
	Ames 1983		Ames 1984		Kanawha 1983		Combined	
	$\bar{X}$	CV	$\bar{X}$	CV	$\bar{X}$	CV	$\bar{X}$	CV
Ear length, cm	17.16	9.16	17.45	8.44	17.62	8.15	17.41	8.59
Yield, q ha^{-1}	27.19	23.74	35.91	15.82	28.82	21.02	30.64	19.82
Stand, no.	18.38	7.00	19.63	10.91	18.60	7.70	18.87	8.81
Ears $plant^{-1}$	0.77	19.19	0.85	14.10	0.81	19.80	0.81	17.71
Plant height, cm	199.00	6.62	203.64	4.56	213.60	4.74	205.41	5.35
Ear height, cm	92.77	11.38	94.54	7.15	96.67	9.24	94.66	9.39
Kernel rows, no.	15.07	6.02	16.06	5.46	15.35	5.63	15.50	5.70
Ear diameter, cm	3.94	5.86	4.24	4.12	3.97	4.97	4.05	4.99
Cob diameter, cm	2.75	6.13	2.87	6.29	2.80	5.54	2.81	6.00
Kernel depth, cm	0.60	16.17	0.69	15.90	0.58	15.60	0.62	15.96
Root lodging, %	15.14	94.98	0.53	381.6	-[a]	-	7.84	131.05
Stalk lodging, %	12.84	75.50	18.45	63.22	-	-	15.65	68.55
Silking date, no.	33.82	5.60	30.09	4.77	-	-	31.95	5.26

[a]Data were not taken for this environment.

Table 23. Combined analysis of variance from three trials for 13 traits of 300 S_1 lines of BSLE

Source of variation	Degrees of freedom	Mean squares			
		Ear length	Yield	Stand	Ears per plant
Environments (E)	2	30.960	12909.346	268.974	1.146
Sets (S)	9	27.321	975.849	11.539	0.255
ExS	18	5.216	136.945	10.090	0.054
Replications/ES	30	6.707	122.490	5.188	0.040
Populations (P)/S	20	956.923**	1388.124**	10.210^{ns}	0.210*
ExP/S	40	22.612**	158.862**	5.493^{ns}	0.038^{ns}
Pooled error a	60	2.737	61.372	3.191	0.027
Lines (G)/P/S	270	18.446**	394.059**	7.859**	0.115**
C0	90	15.446**	347.142**	4.681^{ns}	0.112**
C15S	90	17.925**	450.628**	9.035**	0.095**
C15L	90	21.967**	384.408**	9.862*	0.137**
ExG/P/S	540	3.664**	68.627**	5.738**	0.028**
C0	180	3.564**	74.321**	4.459**	0.026**
C15S	180	2.179**	58.364**	5.488**	0.025**
C15L	180	5.248**	73.196**	7.267**	0.034^{ns}
Pooled error b	810	2.235	36.872	2.763	0.020
C0	270	1.958	42.342	2.346	0.018
C15S	270	1.282	30.260	2.870	0.016
C15L	270	3.465	38.015	3.073	0.027
Total	1799				
Mean		17.41 cm	30.64 q ha^{-1}	18.87	0.81
CV (%)		8.59	19.82	8.81	17.71

*,** Indicate significance at 0.05 and 0.01 probability levels, respectively.

ns Indicates nonsignificance.

Table 23. Continued

Source of variation	Degrees of freedom	Mean squares				
		Plant height	Ear height	Kernel rows	Ear diameter	Cob diameter
Environments (E)	2	33429.390	2291.526	156.634	16.878	2.250
Sets (S)	9	1547.758	1973.152	7.376	0.170	1.062
ExS	18	2800.979	1220.039	1.496	0.113	0.043
Replications/ES	30	457.891	176.066	0.766	0.074	0.032
Populations (P)/S	20	80308.317**	25702.287**	135.797**	4.940**	0.270**
ExP/S	40	2189.959**	1079.178**	3.056**	0.143**	0.053**
Pooled error a	60	208.666	122.264	0.607	0.057	0.029
Lines (G)/P/S	270	1735.496**	1160.593**	12.310**	0.278**	0.129**
C0	90	1785.644**	1303.226**	13.149**	0.218**	0.113**
C15S	90	1681.049**	949.801**	17.978**	0.386**	0.153**
C15L	90	1739.796**	1228.750**	5.803**	0.231**	0.121**
ExG/P/S	540	185.859**	107.812**	1.146**	0.058**	0.032^{ns}
C0	180	193.207**	114.749*	1.188**	0.060**	0.029*
C15S	180	190.929**	86.867**	1.280*	0.052*	0.037^{ns}
C15L	180	173.441^{ns}	121.820^{ns}	0.972**	0.062^{ns}	0.029^{ns}
Pooled error b	810	120.688	78.999	0.780	0.041	0.028
C0	270	113.946	86.407	0.634	0.031	0.022
C15S	270	106.258	50.519	1.008	0.041	0.034
C15L	270	141.859	100.072	0.696	0.050	0.028
Total	1799					
Mean		205.41 cm	94.66 cm	15.50	4.05 cm	2.81 cm
CV (%)		5.35	9.39	5.70	4.99	6.00

Table 23. Continued

Source of variation	Degrees of freedom	Mean squares			
		Kernel depth	Root lodging	Stalk lodging	Silking date
Environments (E)	2	1.889	64066.419	9444.873	4162.688
Sets (S)	9	0.057	280.918	379.079	39.789
ExS	18	0.026	253.426	184.167	17.785
Replications/ES	30	0.015	191.019	127.369	5.516
Populations (P)/S	20	0.814**	934.400^{ns}	1718.057**	737.312**
ExP/S	40	0.022*	845.321**	339.941^{ns}	51.926**
Pooled error a	60	0.011	143.329	273.170	5.021
Lines (G)/P/S	270	0.033**	293.986^{ns}	281.542**	36.900**
C0	90	0.024**	415.288^{ns}	228.680^{ns}	38.458**
C15S	90	0.053**	126.362^{ns}	177.133^{ns}	41.155**
C15L	90	0.022**	336.309*	438.812**	31.086**
ExG/P/S	540	0.012**	256.847**	174.324**	7.172**
C0	180	0.009^{ns}	395.307**	193.237^{ns}	7.252**
C15S	180	0.014^{ns}	121.162^{ns}	149.647**	8.051**
C15L	180	0.013^{ns}	254.07**	180.089*	6.124**
Pooled error b	810	0.010	105.506	115.056	2.826
C0	270	0.007	137.481	144.482	3.182
C15S	270	0.011	92.809	75.184	2.880
C15L	270	0.011	86.228	125.501	2.416
Total	1799				
Mean		0.62 cm	7.84%	15.65%	31.95 days
CV (%)		15.96	131.05	68.55	5.26

For the interaction of the S_1 lines with the environments, only cob diameter had a nonsignificant interaction.

A comparison of the mean performance across environments of the three BSLE subpopulations is shown in Table 24. The trend in response of the S_1 lines of BSLE subpopulations is similar to that noted in evaluation of BSLE subpopulations (Table 12). BSLE C15S exhibited reduced plant height, ear height, stalk lodging, and silking date relative to BSLE C0 but increased number of kernel rows, ear diameter, and kernel depth. Opposite response was shown by BSLE C15L subpopulation. For those traits where the short-ear and long-ear subpopulations diverged in response, asymmetry could be noted with greater change in the short-ear subpopulation except for ear diameter, cob diameter, and kernel depth where BSLE C15L S_1 lines showed greater response. Traits in the short-ear and long-ear subpopulations that changed in the same direction included yield, number of ears per plant, and resistance to root lodging, all of which decreased. The L.S.D. value in Table 24 revealed that the three subpopulations were highly significantly different from each other except for the nonsignificance of the comparison between BSLE C0 and BSLE C15L for root lodging.

Estimates of genetic variances of the three BSLE subpopulations from combined analysis of variance are presented in Table 25. All estimates, except root and stalk lodging, exceeded twice their respective standard errors and were considered statistically different from zero. The genetic variance estimates of any two subpopulations for a certain trait were judged to be significantly different if the

Table 24. A comparison of ear length and 12 other traits of the three BSLE subpopulations based on trials conducted in three environments

Traits	Subpopulations					$LSD_{.01}$
	BSLE C0	BSLE C15S		BSLE C15L		
	$\bar{X}$[a]	$\bar{X}$	ΔX[b]	$\bar{X}$	ΔX	
Ear length, cm	17.64	13.36	-4.28	21.23	3.59	0.02
Yield, q ha^{-1}	35.17	30.19	-4.98	26.56	-8.61	0.54
Stand, no.	19.04	18.97	-0.07	18.60	-0.44	0.03
Ears $plant^{-1}$	0.84	0.81	-0.03	0.77	-0.07	0.0002
Plant height, cm	211.03	167.08	-43.95	238.13	27.10	1.85
Ear height, cm	97.19	73.48	-23.71	113.31	16.12	1.08
Kernel rows, no.	15.30	16.98	1.68	14.21	-1.09	0.005
Ear diameter, cm	4.11	4.29	0.18	3.75	-0.36	0.0005
Cob diameter, cm	2.82	2.85	0.03	2.75	-0.07	0.0003
Kernel depth, cm	0.64	0.72	0.08	0.50	-0.14	0.0001
Root lodging, %	9.59	4.47	-5.12	9.45	-0.14	1.29
Stalk lodging, %	17.07	9.57	-7.50	20.30	3.23	2.46
Silking date, no.	31.16	28.26	-2.90	36.44	5.28	0.04

[a]Observed means.

[b]Difference from BSLE C0.

difference of their variances was more than the sum of the standard errors of their estimates. Based on this criterion, the apparent increase in genetic variance for ear length from BSLE C0 to C15S and C15L was not significant. This maintenance of genetic variability with significant shifts in means is depicted in Figure 10. Nonsignificant differences among the three subpopulations also were found for ears per plant, plant height, ear height, and silking date. On the other

Table 25. Estimates of genetic variances (σ^2_G) of the three BSLE subpopulations for ear length and correlated traits based on trials conducted in three environments

Traits	Subpopulations		
	BSLE C0	BSLE C15S	BSLE C15L
Ear length, cm	1.98 ± 0.38	2.62 ± 0.44	2.78 ± 0.55
Yield, q ha^{-1}	45.47 ± 8.63	65.38 ± 11.20	51.87 ± 9.53
Stand, no.	3.69 ± 1.39	5.91 ± 2.42	1.20 ± 0.49
Ears $plant^{-1}$, no.	0.014 ± 0.003	0.012 ± 0.002	0.017 ± 0.003
Plant height, cm	265.41 ± 44.09	248.35 ± 41.44	261.06 ± 42.86
Ear height, cm	198.08 ± 32.09	143.82 ± 23.39	184.49 ± 30.27
Kernel rows, no.	1.99 ± 0.32	2.78 ± 0.44	0.80 ± 0.14
Ear diameter, cm	0.026 ± 0.005	0.055 ± 0.009	0.028 ± 0.006
Cob diameter, cm	0.014 ± 0.003	0.019 ± 0.004	0.006 ± 0.001
Kernel depth, cm	0.028 ± 0.006	0.015 ± 0.003	0.002 ± 0.001
Root lodging, %	5.00 ± 21.13	1.30 ± 6.45	21.56 ± 15.65
Stalk lodging, %	8.86 ± 11.04	6.87 ± 8.55	64.68 ± 17.48
Silking date, no.	7.80 ± 1.44	8.27 ± 1.54	6.21 ± 1.17

hand, significant differences among the three subpopulations were obtained for kernel rows and kernel depth. A decrease in genetic variability was observed for kernel depth from BSLE C0 to BSLE C15S and BSLE C15L subpopulations.

Comparison of the genetic coefficients of variability in ear length for BSLE C0 and BSLE C15L showed the same values whereas BSLE C15S had an increase (Table 26). For yield, however, the C15 subpopulations have greater values than BSLE C0. For most of the correlated traits, BSLE C15S had the highest coefficients of variability among the

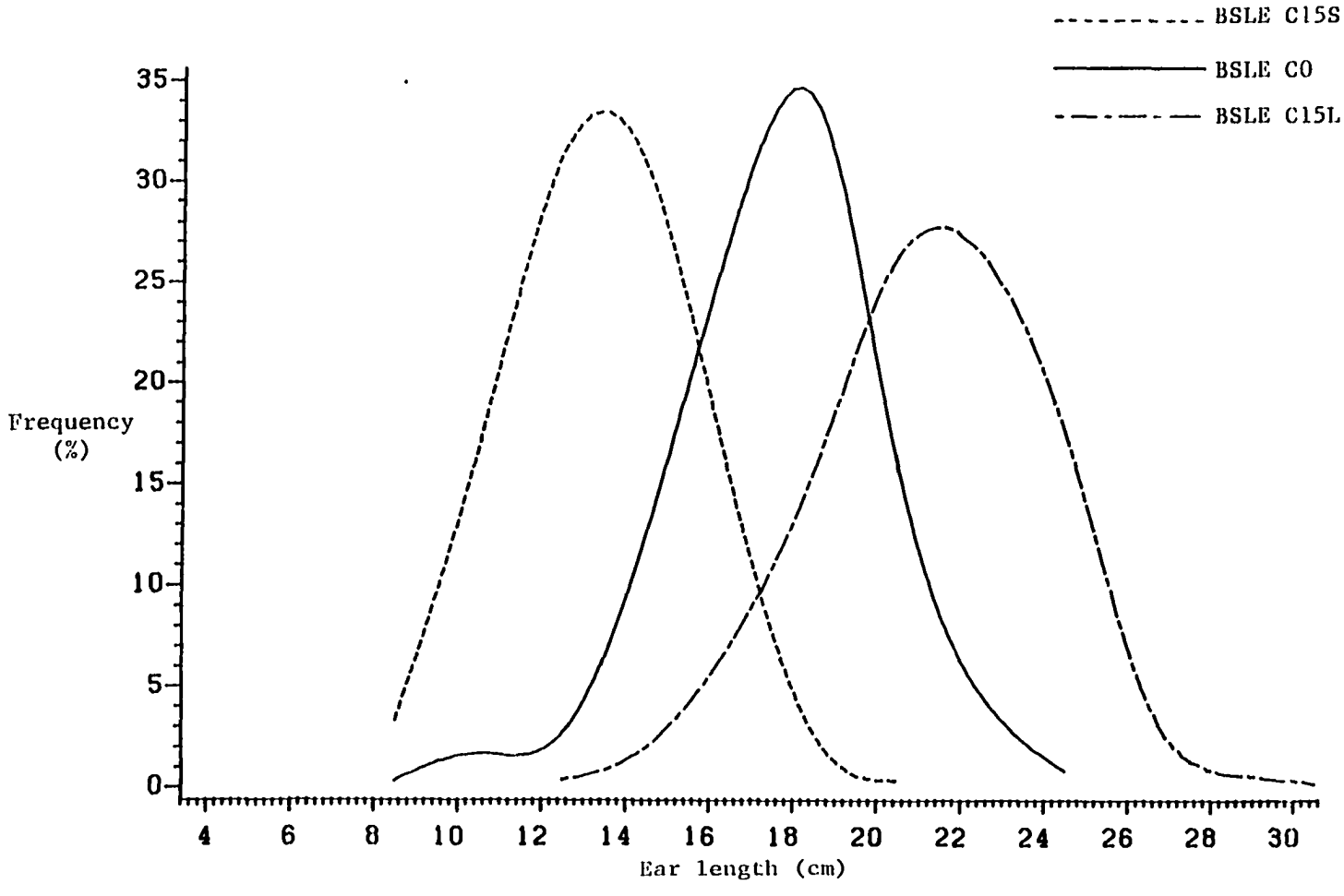

Figure 10. Frequency plot of 100 S_1 progenies for ear length of BSLE original (C0), short-ear (BSLE C15S), and long-ear (BSLE C15L) subpopulations

Table 26. Genetic coefficients of variability (%) of the three BSLE subpopulations for ear length and correlated traits based on trials conducted in three environments

Traits	Subpopulations		
	BSLE C0	BSLE C15S	BSLE C15L
Ear length, cm	7.9	12.1	7.9
Yield, q ha^{-1}	19.2	26.8	27.1
Stand, no.	10.1	12.8	5.9
Ears $plant^{-1}$, no.	14.1	13.5	16.9
Plant height, cm	7.7	9.4	6.8
Ear height, cm	14.5	16.3	12.0
Kernel rows, no.	9.2	9.8	6.3
Ear diameter, cm	3.9	5.5	4.5
Cob diameter, cm	4.2	4.8	2.8
Kernel depth, cm	26.1	17.0	8.9
Root lodging, %	23.3	25.5	49.1
Stalk lodging, %	17.4	27.4	39.6
Silking date, no.	8.9	10.2	6.8

subpopulations evaluated. In most instances, the estimates of the genetic coefficients of variability reflect the changes that occurred for the means and their respective standard errors (Tables 22 and 23). The genetic coefficients of variability were the same for ear length for BSLE C0 and BSLE C15L, but BSLE C15L had greater mean and error mean square. BSLE C15S, however, had a lower mean and error mean square than either BSLE C0 or BSLE C15L.

Estimates of heritability on an individual plant basis are presented in Table 27. Traits which exhibited higher heritability values were plant height (18.4%), ear height (18.4%), number of kernel rows (23.1%), and silking date (18.7%). Root and stalk lodging and plant stand had very low heritabilities of 0.3, 0.6, and 0.2%, respectively. Ear length (8.8%) and the other traits had intermediate levels of heritabilities. Among the three subpopulations, BSLE C15S had the highest heritabilities for most of the traits.

The low and nonsignificant heritability values for root and stalk lodging could probably be ascribed to large error variances (Table 28), which is supported by the large coefficients of variation obtained for these traits (Table 23). For plant stand, the low heritability values were due to less genetic variation (Table 25), rather than due to large error variance.

Table 29 shows that the expression of ear length in BSLE C15S was more consistent across environments than BSLE C0 and BSLE C15L. For yield, the magnitudes of genotype by environment interaction in the three subpopulations were similar. The consistent expression of the other ear traits (ear diameter, cob diameter, and kernel depth) is suggested by their nonsignificant genotype by environment interaction in the three subpopulations except for ear diameter of BSLE C0. BSLE C15L was found to have more consistent measurements for ears per plant, plant and ear height, and stalk lodging, compared with the other BSLE subpopulations.

Table 27. Heritabilities (%) on an individual plant basis for ear length and 12 other traits of the three BSLE subpopulations

Traits	Subpopulations		
	BSLE C0	BSLE C15S	BSLE C15L
Ear length, cm	8.8 ± 1.7	16.5 ± 2.8	7.3 ± 1.4
Yield, q ha^{-1}	9.4 ± 1.8	17.1 ± 2.9	11.5 ± 2.1
Stand, no.	0.2 ± 0.6	1.9 ± 0.8	1.3 ± 0.8
Ears $plant^{-1}$, no.	7.1 ± 1.4	6.6 ± 1.4	5.9 ± 1.2
Plant height, cm	18.4 ± 3.0	18.4 ± 3.1	15.4 ± 2.5
Ear height, cm	18.4 ± 3.0	21.5 ± 3.5	15.4 ± 2.5
Kernel rows, no.	23.1 ± 3.8	21.4 ± 3.4	10.2 ± 1.8
Ear diameter, cm	7.5 ± 1.6	11.7 ± 2.0	5.3 ± 1.1
Cob diameter, cm	5.8 ± 1.2	5.3 ± 1.0	5.2 ± 1.0
Kernel depth, cm	3.3 ± 0.8	5.4 ± 1.1	1.4 ± 0.5
Root lodging, %	0.3 ± 1.4	0.1 ± 0.7	2.2 ± 1.6
Stalk lodging, %	0.6 ± 0.8	0.9 ± 1.1	4.8 ± 1.3
Silking date, no.	18.7 ± 3.5	20.9 ± 3.9	19.3 ± 3.6

Variation among the estimates of genetic variances and heritabilities for BSLE C0 among the three environments could be observed in Table 30. The test at Kanawha showed the highest values of genetic variance and heritabilities for ear length, yield, plant height, and ear height among the three environments. There were some traits (e.g., ear diameter, cob diameter, and silking date) that had similar estimates of genetic variances, but this was not reflected in the estimates of heritabilities. In such cases, the variation in error mean squares

Table 28. Error variances of the three BSLE subpopulations for ear length and correlated traits based on S_1 line trials conducted in three environments in Iowa

Traits	Subpopulations		
	BSLE C0	BSLE C15S	BSLE C15L
Ear length, cm	19.58	12.82	34.65
Yield, q ha^{-1}	423.42	302.60	380.15
Stand, no.	23.46	28.70	30.73
Ears $plant^{-1}$, no.	0.18	0.16	0.27
Plant height, cm	1139.46	1062.59	1418.60
Ear height, cm	864.07	505.19	1000.72
Kernel rows, no.	6.34	10.08	6.96
Ear diameter, cm	0.31	0.42	0.50
Cob diameter, cm	0.22	0.34	0.28
Kernel depth, cm	0.07	0.11	0.11
Root lodging, %	1374.82	928.09	862.28
Stalk lodging, %	1444.81	751.84	1255.02
Silking date, no.	31.82	28.80	24.16

accounted for the difference in heritabilities (Appendix Tables A23, A24, and A25). The very big difference noted between the estimates for genetic variance of root lodging in Ames, 1983 and Ames, 1984 (266.9 vs. 0.4) occurred because of the big difference in the mean root lodging percentages in the two environments. Average root lodging at Ames, 1983 and Ames, 1984 was 15.1 and 0.5%, respectively (Table 22).

Table 29. Genotype by environment interaction variance estimates in three BSLE subpopulations based on S_1 line trials conducted in three environments in Iowa

Traits	Subpopulations		
	BSLE C0	BSLE C15S	BSLE C15L
Ear length, cm	0.80 ± 0.20	0.45 ± 0.13	0.89 ± 0.31
Yield, q ha^{-1}	15.99 ± 4.30	14.05 ± 3.32	17.59 ± 4.17
Stand, no.	1.05 ± 0.25	1.31 ± 0.31	2.10 ± 0.40
Ears $plant^{-1}$, no.	0.004 ± 0.002	0.004 ± 0.002	0.003 ± 0.002
Plant height, cm	39.63 ± 11.24	42.34 ± 11.00	15.79 ± 10.94
Ear height, cm	14.17 ± 7.06	18.17 ± 5.04	10.87 ± 7.69
Kernel rows, no.	0.28 ± 0.07	0.14 ± 0.08	0.14 ± 0.06
Ear diameter, cm	0.015 ± 0.003	0.005 ± 0.003	0.006 ± 0.004
Cob diameter, cm	0.003 ± 0.002	0.001 ± 0.002	0.000 ± 0.002
Kernel depth, cm	0.001 ± 0.001	0.001 ± 0.001	0.001 ± 0.001
Root lodging, %	128.91 ± 30.02	14.18 ± 10.17	83.92 ± 19.27
Stalk lodging, %	24.38 ± 16.13	37.23 ± 11.17	27.29 ± 14.82
Silking date, no.	2.03 ± 0.56	2.58 ± 0.61	1.90 ± 0.48

Genetic correlations among 13 traits in BSLE C0 are presented in Table 31. Computation was based on individual plot data of the 100 S_1 lines evaluated in three environments. Eighteen of 78 coefficients were significant and the highest correlations were obtained between yield and ears per plot (0.86) and between plant height and ear height (0.82). Plant stand and root and stalk lodging did not show any statistically significant correlations with any of the other traits measured. Ear length was significantly correlated with yield (0.35) but silking

Table 30. Genetic variance (σ^2_G) and heritabilities (h^2) on an individual plant basis for 13 traits of BSLE C0 in the three environments based on S_1 progenies

Genetic parameters	Traits and units used					
	Ear length	Yield	Stand	Ears per plant	Plant height	Ear height
	----cm----	q ha^{-1}	----------no.----------		----------cm----------	
σ^2_G						
Ames 1983	3.0±0.6	49.5±10.9	0.5±0.2	0.02±0.01	171.7±36.3	111.4±26.3
Ames 1984	2.0±0.4	69.8±12.9	2.9±0.7	0.01±0.00	396.2±62.4	209.5±35.2
Kanawha 1983	3.7±0.7	80.4±13.6	0.0±0.2	0.02±0.00	408.4±63.0	333.2±58.5
h^2						
Ames 1983	12.4±2.5	10.4±2.3	3.0±1.3	9.4±2.2	11.7±2.5	9.0±2.1
Ames 1984	11.1±2.5	18.1±3.3	7.8±2.0	10.6±2.3	43.1±6.8	27.8±4.7
Kanawha 1983	20.8±3.7	26.5±4.5	0.0±1.0	11.0±2.4	52.2±8.1	86.915.9

Genetic parameters	Traits and units used						
	Kernel rows	Ear diameter	Cob diameter	Kernel depth	Root lodging	Stalk lodging	Silking date
	---no.--	----------cm----------			----------%----------		---no.--
σ^2_G							
Ames 1983	2.0±0.4	0.03±0.01	0.01±0.00	0.002±0.001	266.9±62.9	25.5±15.3	10.2±1.8
Ames 1984	2.9±0.5	0.05±0.01	0.02±0.00	0.004±0.001	0.4±0.7	46.2±22.6	9.4±1.6
Kanawha 1983	1.8±0.3	0.05±0.01	0.02±0.00	0.004±0.001	-[a]	-	-
h^2							
Ames 1983	24.7±4.2	7.7±2.0	3.3±1.4	1.8±1.2	9.0±2.1	2.2±1.3	22.0±3.9
Ames 1984	28.7±4.8	16.4±3.1	17.3±3.2	6.4±1.8	0.6±1.1	2.8±1.4	35.9±5.8
Kanawha 1983	25.0±4.3	28.1±4.7	7.7±2.0	7.2±1.9	-	-	-

[a]Data were not taken for this environment.

Table 31. Genetic correlations[a] among 13 traits for the original BSLE population base

	Ear length	Yield	Stand	Ears per plant	Plant height	Ear height	Kernel rows
Ear length	1.0	0.35±0.12*	0.10±0.60	0.26±0.13*	0.30±0.12*	0.27±0.12*	-0.12±0.1
Yield		1.00	0.57±1.05	0.86±0.05*	0.08±0.12	0.22±0.12	0.04±0.1
Stand			1.00	0.73±1.56	-0.02±0.52	0.24±0.65	0.06±0.5
Ears per plant				1.00	-0.05±0.13	0.14±0.12	-0.08±0.1
Plant height					1.00	0.82±0.04*	0.01±0.1
Ear height						1.00	0.12±0.1
Kernel rows							1.00
Ear diameter							
Cob diameter							
Kernel depth							
Root lodging							
Stalk lodging							
Silking date							

[a]Correlations among ear length to kernel depth, in the order listed, are based or based on two trials.

*Indicates significance at 0.05 probability level.

population based on 100 S_1 progenies

r ht	Kernel rows	Ear diameter	Cob diameter	Kernel depth	Root lodging	Stalk lodging	Silking date
0.12*	-0.12±0.12	-0.26±0.14	-0.19±0.14	-0.19±0.15	-0.93±2.05	0.83±0.55	0.12±0.16
0.12	0.04±0.12	0.34±0.12*	0.06±0.14	0.47±0.12*	1.26±2.70	0.87±0.51	-0.63±0.10*
0.65	0.06±0.53	0.73±1.46	-0.01±0.59	1.19±2.19	0.00±1.29	-0.04±0.71	-0.46±0.31
±0.12	-0.08±0.12	0.12±0.14	-0.02±0.14	0.22±0.15	1.17±1.51	0.80±0.53	-0.46±0.12*
±0.04*	0.01±0.12	0.07±0.13	0.19±0.12	-0.11±0.14	1.51±3.07	0.32±0.34	0.59±0.09*
00	0.12±0.11	0.21±0.12	0.25±0.12*	0.04±0.14	2.03±4.16	0.62±0.40	0.50±0.10*
	1.00	0.50±0.10*	0.45±0.10*	0.27±0.13*	0.32±0.82	0.34±0.39	0.00±0.13
		1.00	0.78±0.06*	0.69±0.08*	0.67±1.55	-0.01±0.41	0.05±0.16
			1.00	0.09±0.15	0.73±1.59	-0.02±0.38	0.19±0.15
				1.00	0.18±0.99	0.01±0.49	-0.17±0.18
					1.00	1.93±5.23	-0.18±0.69
						1.00	-0.38±0.36
							1.00

:ed, are based on three trials, while root and stalk lodging and silking date are

date (-0.63) and kernel depth (0.47) had greater correlations with yield. The correlation between ear length and yield (0.35) was similar to the correlation between yield and ear diameter (0.34).

The traits significantly correlated with ear length included yield (0.35), plant height (0.30), ear height (0.27), and ears per plant (0.26). The other traits were not significantly correlated with ear length, but the sign of the correlation coefficients was consistent with the observations previously made in the evaluation of BSLE subpopulations study.

Later silking genotypes had fewer number of ears per plant and, consequently, less yield as shown by the negative genetic correlation between silking date and ears per plant (-0.46) and between silking date and yield (-0.63).

The phenotypic correlations indicated that ears per plant had the greatest relationship with yield (Table 32). Ear height, ear diameter, cob diameter, kernel depth, and silking date were also significantly correlated with yield. Among the traits correlated with ear length, yield was the most highly correlated (0.38). Ear diameter and kernel depth were the other traits correlated with ear length.

Genetic correlations also were computed for BSLE C15S and BSLE C15L (Tables 33 and 34). In both subpopulations, the correlations of ear length with yield were higher compared to BSLE C0: 0.76 in BSLE C15S and 0.61 in BSLE C15L. Number of ears per plant also showed the strongest relationship with yield in both BSLE subpopulations.

Table 32. Phenotypic correlations[a] among the traits in the original BSLE population based on 100 S_1 progenies

	Ear length	Yield	Stand	Ears per plant	Plant height	Ear height
Ear length	1.00	0.38**	-0.10	0.14	0.16	0.13
Yield		1.00	0.04	0.58**	0.15	0.17*
Stand			1.00	-0.32**	0.02	0.04
Ears per plant				1.00	0.03	0.10
Plant height					1.00	0.06
Ear height						1.00
Kernel rows						
Ear diameter						
Cob diameter						
Kernel depth						
Root lodging						
Stalk lodging						
Silking date						

[a]Correlations among ear length to kernel depth, in the order listed, are based on three trials, while root and stalk lodging and silking date are based on two trials.

*,**Indicate significance at 0.05 and 0.01 probability levels, respectively.

Kernel rows	Ear diameter	Cob diameter	Kernel depth	Root lodging	Stalk lodging	Silking date
-0.02	0.31**	0.14	0.20**	0.13	0.00	-0.15
0.11	0.34**	0.17*	0.21*	0.09	0.04	-0.36**
0.02	-0.11	-0.07	-0.06	-0.11	0.02	0.10
-0.04	0.10	0.04	0.07	0.21	0.03	-0.27**
0.05	0.03	0.01	0.03	0.04	0.00	0.14
0.06	0.05	0.02	0.04	0.14	0.03	0.13
1.00	0.36**	0.23*	0.18*	0.11	0.02	-0.06
	1.00	0.48**	0.63**	0.22**	-0.08	-0.26**
		1.00	-0.37**	0.12	0.10	-0.08
			1.00	0.14	-0.18*	-0.22**
				1.00	-0.22**	-0.02
					1.00	0.14
						1.00

Table 33. Genetic correlations[a] among 13 traits in cycle 15 of BSLE short-ear subpopulati

	Ear length	Yield	Stand	Ears per plant	Plant height	Ear height	Kernel rows	
Ear length	1.00	0.76±0.05*	0.14±0.18	0.60±0.09*	0.47±0.10*	0.37±0.10*	-0.16±0.11	-
Yield		1.00	0.27±0.17	0.82±0.05*	0.40±0.18*	0.40±0.10*	0.01±0.10	
Stand			1.00	0.27±0.21	0.07±0.18	0.12±0.18	0.23±0.17	
Ears per plant				1.00	-0.02±0.13	0.01±0.13	-0.07±0.13	
Plant height					1.00	0.81±0.04*	0.17±0.11	
Ear height						1.00	0.16±0.11	
Kernel rows							1.00	
Ear diameter								
Cob diameter								
Kernel depth								
Root lodging								
Stalk lodging								
Silking date								

[a]Correlations among ear length to kernel depth, in the order listed, are based on th
based on two trials.

*Indicates significance at 0.05 probability level.

subpopulation based on 100 S_1 progenies

Kernel rows	Ear diameter	Cob diameter	Kernel depth	Root lodging	Stalk lodging	Silking date
).16±0.11	-0.01±0.12	-0.11±0.13	0.08±0.13	-0.26±1.04	0.08±0.32	-0.19±0.13
).01±0.10	0.37±0.12*	0.00±0.10	0.54±0.13*	0.23±0.73	0.41±0.38	-0.40±0.11*
).23±0.17	0.12±0.18	0.20±0.19	0.01±0.20	-0.7612.11	0.18±0.54	-0.02±0.19
).07±0.13	0.23±0.12	-0.14±0.14	0.46±0.12*	0.27±0.94	0.28±0.41	-0.68±0.10*
).17±0.11	0.29±0.11*	0.28±0.12*	0.18±0.13	0.69±1.66	-0.19±0.35	0.45±0.11*
).16±0.11	0.21±0.11	0.10±0.12	0.22±0.12	1.03±2.42	-0.15±0.34	0.41±0.11*
1.00	0.41±0.10*	0.42±0.10*	0.23±0.12	0.39±1.06	-0.07±0.30	0.15±0.12
	1.00	0.74±0.07*	0.82±0.05*	0.10±0.62	0.18±0.32	-0.02±0.13
		1.00	0.23±0.14	0.34±1.07	0.26±0.40	0.12±0.15
			1.00	-0.1410.85	0.04±0.37	-0.13±0.14
				1.00	-1.36±3.77	-0.09±0.65
					1.00	-0.33±0.37
						1.00

based on three trials, while root and stalk lodging and silking date are

Table 34. Genetic correlations[a] among 13 traits in cycle 15 of BSLE long-ear subp

	Ear length	Yield	Stand	Ears per plant	Plant height	Ear height	Kern row
Ear length	1.00	0.61±0.09*	0.20±0.25	0.62±0.10*	-0.05±0.13	-0.06±0.13	-0.10
Yield		1.00	0.55±0.23	0.85±0.05*	-0.17±0.12	-0.04±0.12	0.04
Stand			1.00	0.20±0.27	0.02±0.22	0.12±0.22	-0.02
Ears per plant				1.00	-0.17±0.12	0.00±0.13	0.01
Plant height					1.00	0.79±0.04*	-0.08
Ear height						1.00	-0.02
Kernel rows							1.0
Ear diameter							
Cob diameter							
Kernel depth							
Root lodging							
Stalk lodging							
Silking date							

[a]Correlations among ear length to kernel depth, in the order listed, are base based on two trials.

*Indicates significance at 0.05 probability level.

ng-ear subpopulation based on 100 S_1 progenies

t	Kernel rows	Ear diameter	Cob diameter	Kernel depth	Root lodging	Stalk lodging	Silking date
.13	-0.10±0.13	0.11±0.14	0.11±0.14	0.06±0.19	0.03±0.30	0.20±0.18	-0.38±0.13*
.12	0.04±0.13	0.43±0.11*	0.12±0.13	0.73±0.13*	-0.11±0.17	0.37±0.15*	-0.82±0.06*
.22	-0.02±0.23	0.58±0.25*	0.57±0.26*	0.34±0.34	-0.61±0.40	0.00±0.23	-0.20±0.19
.13	0.01±0.13	0.14±0.14	-0.03±0.14	0.36±0.18*	0.30±0.29	0.40±0.15*	-0.71±0.08*
.04*	-0.08±0.12	-0.20±0.12	-0.11±0.12	-0.27±0.17	0.01±0.24	-0.03±0.15	0.47±0.11*
)	-0.02±0.12	-0.06±0.13	-0.04±0.13	-0.08±0.17	0.22±0.23	0.22±0.15	0.43±0.11*
	1.00	0.48±0.11*	0.57±0.10*	0.13±0.18	0.05±0.26	0.03±0.16	0.02±0.14
		1.00	0.90±0.05*	0.72±0.10*	0.06±0.28	-0.17±0.17	-0.27±0.14
			1.00	0.35±0.20	0.24±0.32	-0.44±0.18	0.03±0.15
				1.00	-0.20±0.42	0.25±0.24	-0.61±0.18
					1.00	-0.03±0.31	0.09±0.25
						1.00	-0.19±0.15
							1.00

ed, are based on three trials, while root and stalk lodging and silking date are

From the estimates of heritabilities and genetic correlations in BSLE C0, predicted gains due to selection and efficiency of indirect selection were computed and are presented in Tables 35 and 36, respectively. Table 36 shows that only root lodging, stalk lodging, and plant stand had indirect selection efficiencies which were greater than 100%. The values for each trait, however, are questionable because they have nonsignificant heritabilities (Table 27) and the genetic correlation with yield is relatively low. Examining only the traits which showed significant heritabilities and genetic correlation with yield, none was found to be good enough to warrant indirect selection for yield. The best value for indirect selection efficiency was 92.6% for ears per plant, which was followed by 61.3% for kernel depth, -50.4% for silking date, 35.7% for ear length, and 35.6% for ear diameter.

The predicted response in correlated traits with direct selection for ear length and the actual results obtained in BSLE C15S and BSLE C15L are listed in Table 37. For the prediction of direction of change, the prediction equation was successful in the short-ear subpopulation except for root lodging. In the long-ear subpopulation, opposite direction of change resulted for yield, plant stand, and ears per plant.

The predictions overestimated the response for ear length in the S_1 progenies. Similar trends occurred for the other ear traits, which included ear diameter, cob diameter, and kernel depth. For some plant traits, however (e.g., plant height, ear height, stalk lodging, and silking date), there was an underestimation of response to selection. Also, contrary to the expected increase in yield in the long-ear

Table 35. Direct and correlated responses expected from mass selection in Iowa Long Ear Synthetic (BSLE)

Traits directly selected	Ear length	Yield	Stand	Ears per plant	Plant height	Ear height
	cm	q ha^{-1}	------no.--------		-------cm---------	
Ear length	0.40	0.67	0.01	0.01	1.37	1.07
Yield	0.14	1.95	0.04	0.38	0.88	0.02
Stand	0.01	0.14	0.01	-0.01	0.12	0.00
Ears per plant	0.09	1.46	0.04	-0.20	0.49	-0.03
Plant height	0.17	0.22	0.00	6.60	4.68	0.01
Ear height	0.15	0.59	0.02	5.42	5.70	0.07
Kernel rows	-0.08	0.12	0.01	0.08	0.75	0.64
Ear diameter	-0.09	0.58	0.04	0.30	0.75	0.18
Cob diameter	-0.06	0.09	0.00	0.69	0.80	0.14
Kernel depth	-0.04	0.54	0.04	-0.30	0.09	0.06
Root lodging	-0.06	0.42	0.00	0.01	1.22	1.35
Stalk lodging	0.08	0.39	0.00	0.01	0.35	0.55
Silking date	0.06	-1.58	-0.12	-0.02	3.58	2.50

Correlated traits						
Kernel rows	Ear diameter	Cob diameter	Kernel depth	Root lodging	Stalk lodging	Silking date
no.	cm			%		no.
-0.05	-0.01	-0.01	0.00	-0.51	0.61	0.08
0.02	0.00	0.00	0.01	0.73	0.67	-0.46
0.00	0.00	0.00	0.00	0.00	-0.01	-0.14
0.01	0.00	0.00	0.00	0.65	0.59	-0.32
0.00	0.01	0.01	0.00	1.19	0.34	0.58
0.01	0.01	0.01	0.00	1.59	0.64	0.49
0.04	0.02	0.02	0.01	0.32	0.45	0.00
0.04	0.02	0.02	0.01	0.34	-0.01	0.03
0.03	0.03	0.03	0.00	0.36	-0.01	0.12
0.02	0.00	0.00	0.01	0.06	0.00	-0.07
0.02	0.01	0.00	0.00	0.12	0.31	-0.03
0.04	0.00	0.00	0.00	0.32	0.22	0.08
0.00	0.00	0.01	0.00	-0.17	-0.46	1.14

Table 36. Efficiency of indirect selection (%) expected from mass selection in Iowa Long Ear Synthetic (BSLE)

Traits directly selected	Ear length	Yield	Stand	Ears per plant	Plant height	Ear height
Ear length	100.0	34.3	76.5	28.6	20.8	18.7
Yield	36.3	100.0	448.6	99.4	5.7	15.5
Stand	1.3	7.2	100.0	10.6	-0.2	2.2
Ears per plant	22.8	75.0	498.7	100.0	-3.1	8.6
Plant height	43.1	11.2	-26.5	07.9	100.0	82.0
Ear height	38.9	30.4	267.9	22.5	82.2	100.0
Kernel rows	-18.9	6.1	74.8	-15.2	1.2	13.2
Ear diameter	-23.6	30.1	518.5	12.7	4.5	13.2
Cob diameter	-15.4	4.6	-.50	-1.7	10.5	14.0
Kernel depth	-11.4	27.8	555.9	15.1	-4.5	1.6
Root lodging	-20.7	26.4	0.1	25.7	23.3	31.6
Stalk lodging	25.0	24.4	-2.4	23.6	6.8	13.0
Silking date	20.9	-99.6	-166.2	-75.3	68.7	58.5

Correlated traits						
Kernel rows	Ear diameter	Cob diameter	Kernel depth	Root lodging	Stalk lodging	Silking date
-7.2	-27.9	-23.7	-31.0	-418.4	278.5	7.5
2.5	37.7	7.6	79.8	602.6	307.5	-40.1
0.5	10.4	-0.1	25.5	0.5	-5.8	-12.8
-4.6	12.0	-2.1	32.6	538.1	272.2	-27.8
1.0	11.1	33.6	-25.3	977.6	156.6	50.9
10.5	32.4	44.8	9.0	1305.5	295.4	42.7
100.0	87.3	90.0	72.5	266.4	204.9	0.4
28.2	100.0	89.6	103.9	282.6	-3.6	2.8
22.4	68.8	100.0	11.9	296.4	-5.8	10.3
10.2	45.4	6.8	100.0	48.7	1.1	-6.0
4.0	16.0	18.2	6.6	100.0	143.8	-2.4
5.5	-0.4	-0.6	0.3	260.3	100.0	-6.8
0.3	9.0	35.6	-46.4	-138.6	-212.0	100.0

Table 37. Predicted[a] and observed response (units cycle^{-1}) after 15 cycles of mass selection for ear length in Iowa Long Ear Synthetic (BSLE)

Traits	Subpopulations			
	BSLE C15S		BSLE C15L	
	Predicted	Observed	Predicted	Observed
Ear length, cm	-0.40	-0.28	0.40	0.24
Yield, q ha^{-1}	-0.67	-0.33	0.67	-0.57
Stand, no.	-0.01	-0.01	0.01	-0.03
Ears plant^{-1}	-0.01	-0.00	0.01	1.01
Plant height, cm	-1.37	-2.93	1.37	1.21
Ear height, cm	-1.07	-1.58	1.07	1.08
Kernel rows, no.	0.05	0.11	-0.05	-0.07
Ear diameter, cm	0.01	0.01	-0.01	-0.02
Cob diameter, cm	0.01	0.00	-0.01	-0.01
Kernel depth, cm	0.00	0.01	0.00	-0.01
Root lodging, %	0.51	-0.34	-0.51	-0.01
Stalk lodging, %	-0.61	-0.50	0.61	0.22
Silking date, no.	-0.08	-0.19	0.08	0.35

[a]Same magnitude of values for BSLE short-ear and long-ear subpopulations but with opposite signs.

subpopulation and decrease in the short-ear subpopulation, both the subpopulations decreased in yield. The only close agreements obtained between the observed and predicted values were for plant stand for short-ear subpopulation and cob diameter in the long-ear subpopulation.

The expected responses from continued mass selection for ear length in BSLE C15S and C15L are shown in Table 38. Further asymmetrical

Table 38. Expected response from mass selection for ear length in cycle 15 subpopulations of BSLE

Traits	Subpopulations	
	BSLE C15S	BSLE C15L
Ear length, cm	-0.62	0.42
Yield, q ha^{-1}	-2.34	0.68
Stand, no.	-0.04	0.13
Ears per plant	-0.02	0.58
Plant height, cm	-2.82	-0.07
Ear height, cm	-1.71	-0.08
Kernel rows	0.10	-0.11
Ear diameter, cm	0.00	0.10
Cob diameter, cm	0.01	0.10
Kernel depth, cm	0.00	0.04
Root lodging, %	-0.04	0.06
Stalk lodging, %	-0.17	-0.30
Silking date, no.	0.02	-0.15

changes in the short-ear and long-ear selections are predicted. Yield is expected to increase in the long-ear subpopulation and decrease in the short-ear subpopulation. Opposite directions of response are predicted also for plant stand, ears per plant, number of kernel rows, root lodging, kernel depth, and silking date. The expected direction of change, however, for silking date in C15 subpopulations is the reverse of BSLE C0 (Table 37). Increases in ear and cob diameter and kernel depth

and decreases in plant and ear height are expected for both the short-ear and long-ear subpopulations.

DISCUSSION

Due to the low heritability of yield, indirect selection using another trait with a higher heritability and a high correlation with yield has been suggested. Among the traits that met these requirements were prolificacy, ear length, and kernel depth (Hallauer and Miranda, 1981). Studies have been conducted investigating the effect of selecting prolific types (Gardner, 1961; Lonnquist, 1967; Hallauer and Sears, 1969; Torregroza, 1973; Lantin, 1980), but limited information is available for determining the effects of selection for kernel depth and ear length. This study was conducted to obtain a better understanding of the effect of selecting for ear length by use of mass selection.

Iowa Long Ear Synthetic (BSLE) was developed in 1957 in response to early reports of greater importance of ear length than the other traits as a major yield component in some maize populations. Since its synthesis, three studies had been conducted to monitor the effects of mass selection for ear length in BSLE. Hallauer (1968) determined the genetic variance in the original BSLE after three generations of random mating its 12 component inbred lines. Cortez-Mendoza (1977) and Cortez-Mendoza and Hallauer (1979) evaluated the performance of the diverged subpopulations of BSLE after 10 cycles of mass selection. Their study will be referred to hereon as C10 study. This study investigated the progress of selection after 15 cycles. The BSLE population is undergoing its 20th cycle of divergent selection at the present time.

Hallauer (1968), using Design I mating and testing the generated families at three locations in 1966, reported that the total genetic

variance for ear length, yield, and most of the other traits measured in BSLE C0 was due to additive effects. Heritability on a per plant basis for ear length was found to be about three times greater than yield (7.6 vs. 2.6), but both estimates were considered relatively low. Progress from mass selection was, therefore, predicted at a slow rate; i.e., 0.34 cm year^{-1}. Slow rates of response to selection are expected for quantitative traits. Ear length was selected by a method that was based only on the phenotypic appearance of individual genotypes in only one environment. Confounding effects of the environment leading to slow progress could be expected and this was demonstrated in the C15 study by the significant values of genotype by environment interaction variance (Table 29) for ear length and most of the other traits.

The rate of change for ear length and the other traits in BSLE after 10 cycles was not found to be symmetrical in the opposite directions of selection. Ear length was reduced in the short-ear subpopulation by 0.64 cm year^{-1} which was twice the rate for increased ear length of the long-ear subpopulation. Another deviation from prediction was the yield trend. Based on genetic correlations, yield was expected to increase in the long-ear subpopulation and decrease in short-ear subpopulation. The long-ear subpopulation, however, did not significantly change in yield, but the short-ear subpopulation decreased in yield as predicted. The expected directions of changes for the other traits in the two subpopulations, however, were supported by the observed data; i.e., smaller ear diameter, shallower and lighter kernels, fewer number of kernel rows, and taller plants occurred with selection for longer ears. The opposite trends were observed with selection for shorter ears.

Results of the C15 study revealed similar trends of response as in the C10 study. The rate of change for ear length and the other traits was primarily linear (Figures 1 to 9). The linear regression sum of squares for ear length accounted for 82.5% of the total observed variation (Appendix Table A8). Highly significant linear regression sum of squares for most of the traits suggested adequacy of linear model in describing response to selection (Tables 11 and 14).

Asymmetry of response also was obtained for ear length in the C15 study. The long-ear subpopulation increased by 0.38 cm $year^{-1}$ (1.9%), whereas the short-ear subpopulation decreased by 0.46 cm $year^{-1}$ (2.3%). Traits correlated with ear length (Table 30) also exhibited asymmetrical responses (Table 12). The regression coefficients for advanced cycles and crosses of BSLE C0 to advanced cycles (Tables 12 and 15) revealed higher values for short-ear selection compared to the long-ear selection. Examination of the regression coefficients by gene frequency analysis showed the same trend (Table 19). Traits detected by gene frequency analysis to be significantly altered by selection were ear length, ear diameter, root lodging, silking time, and plant and ear heights. All of these traits exhibited asymmetrical response to selection as depicted in Figures 1, 2, 5, 6, 7, and 8.

Falconer (1981) discussed eight possible causes of asymmetrical response in divergent selection: random drift, inbreeding depression, maternal effects, nonuniform selection differential, indirect selection, genetic asymmetry, scalar asymmetry, and genes with large effects.

Random drift and inbreeding depression should not be major causes for asymmetrical response because of the large effective population size used (300 plants selected out of 4000) in each cycle of selection. The results of gene frequency analysis (Table 19) showed that inbreeding depression was not significant for ear length and most of the other traits.

Maternal effects, as explained by Falconer (1981), had greater relevance in animals. In corn, maternal effects are generally not significant and most likely would not explain the asymmetrical response.

The selection differential may differ between the upward and downward selected lines for the following reasons: (1) natural selection may aid artificial selection in one direction or hinder it in the other; (2) the fertility may change so that a higher intensity of selection is achieved in one direction than in the other; and (3) the variance may change as a result of the change of mean; i.e., the selection differential will increase as the variance increases and vice versa. This is termed scale effect. The same selection intensity was practiced in both the short-ear and long-ear subpopulations of BSLE, and there were no observable differences in their seed emergence and seedling vigor. Greater response also was observed in the short-ear than in the long-ear subpopulation. Hence, scale effects do not seem to be important. With these observations, nonuniform selection differential does not seem likely to be a major factor for asymmetry of response to selection.

Indirect selection would cause asymmetry if the measured character is not linearly related to the selection criterion. In BSLE, ear length

was the trait directly selected and evaluated; therefore, this factor is not relevant to the observed asymmetry for ear length. This, however, may be helpful in explaining the asymmetrical trends for the other traits not found to be significantly correlated with ear length: kernel row number, ear diameter, cob diameter, kernel depth, root and stalk lodging, and silking time (Tables 12 and 30).

Gene frequency for longer ears may have been greater than 0.5 in the original BSLE population because it was synthesized from 12 long-eared inbred lines. Consequently, greater response would be expected with short-ear selection than in the opposite direction. Hence, genetic asymmetry must be a major reason for the asymmetrical response observed in BSLE after 15 cycles of continuous divergent mass selection. This was also the main factor cited by Cortez-Mendoza (1977) in explaining the asymmetrical trend in the C10 study.

Scalar asymmetry occurs when the genetic and environmental variations are skewed in either different degrees or in different directions. The difference in skewness could be due either to scale effects or to genotype by environment interaction. Scale effect would not be a factor as discussed previously. Genotype by environment interaction, however, would be a possible explanation. Genotype by environment interaction for ear length was significant in BSLE C15S and C15L (Table 29).

The opposite skewness of genetic and environmental variance could be established. Due to genetic asymmetry of BSLE C0, the genetic variance is expected to be skewed to the high side; i.e., less genetic variation for long ears. The skewness of the environmental variance,

on the other hand, to the low side could be deduced from Table 28 which showed that BSLE C15S had less error variance than BSLE C15L. Populations with higher genetic values (long-ear) are, therefore, expected to have lower heritability because of less genetic variation and more environmental variation. The reverse would occur for short-ear populations, i.e., heritability would be higher. This situation actually occurred, as shown in Table 27: BSLE C15S had heritability of 16.5 ± 2.8% while BSLE C15L had 7.3 ± 1.9%. With lower heritability, long-ear selection would have slower response compared to short-ear selection and asymmetrical response would result.

The aspect of the extent of effects of genes is more relevant to the explanation of the onset of asymmetry. If there is genetic asymmetry in the original population, asymmetry could result with genes having smaller effects and would occur after a longer time. With genes having larger effects, however, genetic asymmetry would tend to exhibit immediate asymmetrical response. In BSLE, there was a gradual divergence in ear length, which is illustrated in Figure 1 and in Appendix Table A8. Hence, genes for ear length must have smaller effects.

Falconer (1981) defined heterosis (h) as $h = (p-r)^2 d$, where p and r are the corresponding gene frequencies in the two concerned populations and d is the dominance effect. The formula shows that dominance type of gene action and difference in gene frequencies are needed for the expression of heterosis. After 15 cycles, heterosis was detected for ear length (Table 19). This result suggests that a certain level of dominance is present in the expression of ear length and that the two

subpopulations are significantly different in their gene frequencies. With the linearity in response of BSLE to the 15 cycles of mass selection, significant change in gene frequency must have occurred in the two BSLE subpopulations. This was shown to have occurred by the gene frequency analysis (Table 19). The AL+DL term, which is the effect due to selection, was significant for ear length and most of the other traits in the two BSLE subpopulations.

After 15 cycles of mass selection, grain yield decreased in both the short-ear and long-ear subpopulations. This could be explained by examination of the significant regression coefficients listed in Table 12. In the long-ear subpopulation, there was a significant increase in ear length, but reduction also occurred for number of kernel rows and ear diameter (due to change in kernel depth rather than to cob diameter). With the increase in plant height of BSLE long-ear subpopulation, there was also an increased incidence of root lodging, which could have contributed to yield loss.

With the shorter plant height of short-ear subpopulation, there was a greater resistance to root and stalk lodging. There was also an increase in ear diameter and number of kernel rows. Such favorable effects, however, did not compensate for the significant reduction in ear length and number of ears per plant leading ultimately to a yield reduction.

One objective of this study was to measure the genetic variation in BSLE available after 15 cycles of divergent selection. With linear response of BSLE subpopulations observed in C10 and C15 studies,

information was desired to determine if there was adequate genetic variability in the advanced subpopulations to sustain further progress. Recurrent selection to improve breeding populations is based on the maintenance of genetic variability while improving the average performance of the population. The results obtained in this study suggested that sufficient genetic variance for ear length was present in BSLE C15S (2.62 ± 0.44) and C15L (2.78 ± 0.55) compared with BSLE C0 (1.98 ± 0.38) to expect further response to selection. Although there was an apparent increase in both subpopulations, the estimates were not statistically significant. These estimates were based on S_1 progenies. It should be emphasized that yield was reported for the C15 study on a per plot basis vs. the per plant basis in the C10 study. This was because in the C15 study, all plants in a plot were harvested whereas in the C10 study only competitive plants were harvested. In the C15 study, plant stands of the three subpopulations were not statistically different from each other as well as the plant stand of the lines within BSLE C0 (Table 23). Expressing, therefore, the results on per plant basis by dividing plot yield by plant stand would be expected to give the same degree of genetic variation among lines within the population as when yield was reported on per plant basis. All the other traits, except plant stand and silking date, were reported on per plant basis as in the C10 study.

Due to the larger effective population size used in mass selection, genetic variability is usually maintained for a longer time compared to other breeding methods involving more intense selection. With larger population size, the successive cycles of intermating the selected

genotypes will provide opportunities for more recombination and breaking up of linkages. As a result, genetic variability could be maintained for a longer time. Mulamba (1981) observed that genetic variance for yield in maize variety Krug was greater in mass selected population after 14 cycles (65.50 ± 11.48) compared to populations improved by eight cycles of half-sib (52.91 ± 8.54) or S_1 (27.99 ± 6.08) selections. The original Krug had genetic variance equal to 62.50 ± 11.11.

From the estimates of different genetic parameters in BSLE C0, the responses for ear length and correlated traits were predicted. Most of the predicted values showed deviations from the actual results and for ear length the response was overestimated (Table 36). Such a discrepancy could be due to nonadditive genetic variance bias in the estimate of additive genetic variance using S_1 lines. Hallauer (1968) and Cortez-Mendoza and Hallauer (1979) used Design I, which could separate additive from dominance variance, in BSLE C0 and obtained close agreement between the actual and expected responses. Predicted gain for ear length was 0.34 cm $year^{-1}$, and the actual result was 0.32 cm $year^{-1}$.

The genetic correlations computed among the traits (Table 32) in BSLE C0 suggested that grain yield could be increased more by selecting for prolific types rather than by selecting for longer ears. Number of ears per plant (7.1%) and ear length (8.8%) had comparable heritabilities. Efficiency of indirect selection using prolificacy was, however, computed to be still less than 100%. This could be attributed to the lower heritability of number of ears per plant (7.1%) compared to yield (9.4%).

The genetic correlations computed in BSLE C15S and C15L could explain the apparent reversal of predicted silking date responses shown in BSLE C0. In contrast to the positive genetic correlation between ear length and silking date in BSLE C0, the correlation has become negative in both BSLE C15S and C15L (Tables 30, 33, and 34). The genetic correlations in BSLE C15L also have become positive, although nonsignificant, between ear length and ear and cob diameter, between ear length and kernel depth, and between ear length and plant and ear height. This has led to contrasting trends of predicted response in BSLE C15L from that of BSLE C0. Because no changes were predicted for ear diameter and kernel depth in BSLE C15S, this suggests that the limits for extension of most of the ear traits and silking date in both subpopulations have been reached as well as the limits for plant and ear height and ear and cob diameter in the long-ear subpopulation although the limit for ear length has not been attained. It is suggested, therefore, that whenever the apparent selection limit for ear length is reached in this long-term mass selection program, a genetic variance study and reverse selection should be conducted, as conducted by Dudley (1977) in maize and Ceccarelli and Grando (1981) in barley. This is to evaluate how the fitness reducing effects of artificial selection have been counteracted by natural selection through some genetic mechanisms (Falconer, 1981).

SUMMARY AND CONCLUSIONS

The response of BSLE to 15 cycles of divergent mass selection for ear length was evaluated. Cycles 0, 3, 6, 9, 12, and 15 of both the short-ear and long-ear subpopulations, crosses of BSLE original to advanced cycles, and crosses of corresponding cycles of the two subpopulations were tested in seven environments in 1982 and 1983. Data were recorded for ear length, grain yield, ear diameter, cob diameter, kernel depth, number of kernel rows, number of ears per plant, stand count, root lodging, stalk lodging, ear droppage, grain moisture content, silking date, plant height, and ear height. Data from combined experiments were subjected to regression analysis using the models proposed by Eberhart (1964) and Hammond and Gardner (1974).

Results of the analyses showed that mass selection was effective in changing the frequencies of genes controlling ear length in BSLE. The rates of responses were linear, and asymmetry was noted with greater response in the short-ear subpopulation. Among the eight possible causes cited by Falconer (1981) for asymmetrical response, genetic and scalar asymmetries were the main reasons for asymmetry of response to mass selection for ear length in BSLE. There was genetic asymmetry because BSLE was synthesized from long-eared inbred lines. Greater response would, therefore, be expected from selection for short ears because, essentially, no previous selection had been conducted for shorter ears. Scalar asymmetry was due to differential skewness of genetic and environmental variances. Genetic variance was concluded

to be skewed to the right because of higher frequency of long-eared genotypes; i.e., genetic asymmetry. Environmental variance was skewed to the left as revealed by smaller error variance for BSLE C15S compared with BSLE C15L. With less genetic variation, greater environmental variance and hence lower heritability for long ears, less response was expected compared to short-ear subpopulation. It was also concluded that the genes for ear length had small effects because the occurrence of asymmetry was not immediate.

With an increase in ear length, there were significant correlated reductions in ear diameter and number of kernel rows and increases in plant height, ear height, lodging, and silking date. Opposite trends of change occurred for the short-ear subpopulation. Yield, however, decreased in both subpopulations. Yield reduction in the short-ear subpopulation was explained by the decrease in ear length and number of ears per plant which were not compensated by the increase in number of kernel rows and ear diameter. In the long-ear subpopulation, the increase in ear length did not compensate for the reduction in kernel depth and number of kernel rows.

After 15 cycles, heterosis was detected for ear length. This suggested that significant changes in gene frequencies for ear length in the two subpopulations have occurred and that dominance type of gene action was present.

Genetic variability in BSLE C0, C15S, and C15L was determined from use of 100 S_1 lines per population tested in three environments. Genetic variability was maintained in the two subpopulations after 15 cycles of

mass selection. Consequently, progress in terms of change in ear length was expected from further mass selection.

Based on estimates of heritability and genetic correlation, direct and correlated responses and efficiencies of indirect selection were computed. From the BSLE C0 data, the predicted response did not agree with the actual results. This was ascribed to nonadditive genetic variance bias in estimating the true additive genetic variance of the population by use of S_1 lines. The computed expected responses from estimates on BSLE C15S and C15L showed asymmetrical trends with greater response in the short-ear subpopulation.

Computed efficiencies of indirect selection showed that in BSLE C0 no alternative trait to improve yield indirectly would be better than when selection were for yield itself. This was ascribed to insufficient magnitude of heritabilities and/or genetic correlations of the other traits to yield. Determination of genetic variance and reverse selection were suggested whenever the apparent selection limit has been attained to understand how the genetic make up of the population was affected by long-term mass selection.

LITERATURE CITED

Acosta, A. E., and P. L. Crane. 1972. Further selection for lower ear height in maize. Crop Sci. 12:165-167.

Anderson, R. L., and T. A. Bancroft. 1952. Statistical theory in research. McGraw-Hill Inc., New York.

Ariyanayagam, R. P., C. L. Moore, and V. R. Carangal. 1974. Selection for leaf angle in maize and its effect on grain yield and other characters. Crop Sci. 14:551-556.

Beatson, R. A., E. A. Wernsman, and R. C. Long. 1984. Divergent mass selection for carotenoids in a flue cured tobacco population. Crop Sci. 24:67-71.

Benoff, F. H., and J. A. Renden. 1983. Divergent selection for mature body weight in dwarf white leghorns. 1. Growth and reproductive responses to selection. Poultry Sci. 62:1931-1937.

Bohren, B. B., W. G. Hill, and A. Robertson. 1966. Some observations on asymmetrical correlated responses to selection. Genetical Research Cambridge 7:44-57.

Ceccarelli, S., and M. Falcinelli. 1978. Divergent selection for culm length in barley. II. Correlated responses to selection. Z. Pflanzenzuchtg. 80:299-310.

Ceccarelli, S., and S. Grando. 1981. Divergent selection for culm length in barley. III. Responses to six cycles of within-families selection. Z. Pflanzenzuchtg. 86:56-68.

Clucas, C. C. 1984. Effects of visual selection among and within S_1 lines of maize on S_2 line and testcross performance. Ph.D. dissertation. Iowa State University, Ames, Iowa.

Cockerham, C. C. 1963. Estimation of genetic variances. In W. D. Hanson and H. F. Robinson (eds.) Statistical genetics in plant breeding. Nat. Acad. Sci. Nat. Res. Counc. Pub. 982:53-93.

Colleau, J. J., J. Lefevbre, M. Dupont, C. Felgines, and W. Wimitzky. 1983. Divergent selection for milk yield in Normandy cattle. 1. Effects on beef production in young bulls. Genetique, Selection, Evolution 15:119-145.

Compton, W. A., R. F. Mumm, and B. B. Mathema. 1979. Progress from adaptive mass selection in incompletely adapted maize populations. Crop Sci. 19:531-533.

Cortez-Mendoza, H. 1977. Evaluation of ten generations of divergent mass selection for ear length in Iowa Long Ear Synthetic of maize. Ph.D. dissertation. Iowa State University, Ames, Iowa.

Cortez-Mendoza, H., and A. R. Hallauer. 1979. Divergent mass selection for ear length in maize. Crop Sci. 19:175-178.

Crosbie, T. M., and R. B. Pearce. 1982. Effects of recurrent phenotypic selection for high and low photosynthesis on agronomic traits in two maize populations. Crop Sci. 21:736-740.

Crosbie, T. M., R. B. Pearce, and J. J. Mock. 1981. Recurrent phenotypic selection for high and low photosynthesis in two maize populations. Crop Sci. 21:736-740.

Cross, H. Z. 1981. Use of R-nj aleurone color to improve grain yields of early maize. Crop Sci. 21:751-754.

Dickerson, G. E. 1959. Techniques for research in quantitative genetics. pp. 56-105. In Techniques and procedures in animal production research. American Society of Animal Production, Urbana, Illinois.

Draper, N. R., and H. Smith. 1966. Applied regression analysis. John Wiley and Sons, Inc., New York.

Dudley, J. W. 1977. Seventy-six generations of selection for oil and protein percentage in maize. Pp. 459-473. In Proc. Int. Conf. Quant. Genet. Iowa State University Press, Ames, Iowa.

Dudley, J. W., and R. J. Lambert. 1969. Genetic variability after 65 generations of selection in Illinois high oil, low oil, high protein and low protein strain of Zea mays L. Crop Sci. 9:179-181.

Dudley, J. W., R. J. Lambert, and D. E. Alexander. 1974. Seventy generations of selection for oil and protein concentration in the maize kernel. Pp. 181-212. In J. W. Dudley (ed.) Seventy generations of selection for oil and protein in maize. Crop Science Society of America, Madison, Wisconsin.

Eberhart, S. A. 1964. Least squares method for comparing progress among recurrent selection methods. Crop Sci. 4:230-231.

Eberhart, S. A., M. N. Harrison, and F. Ogada. 1967. A comprehensive breeding system. Der Züchter 37:169-174.

Falconer, D. S. 1953. Selection for large and small size in mice. J. Genetics 51:470-501.

Falconer, D. S. 1981. Introduction to quantitative genetics. Longman Inc., New York.

Gardner, C. O. 1961. An evaluation of effects of mass selection and seed irradiation with thermal neutrons on yield of corn. Crop Sci. 1:241-245.

Gardner, C. O. 1968. Mutation studies involving quantitative traits. Gamma Field Symposium 7:57-77.

Genter, C. F. 1976. Mass selection in a composite of intercrosses of Mexican races of maize. Crop Sci. 16:556-558.

Goodman, M. M. 1965. Estimates of genetic variance in adapted and exotic populations of maize. Crop Sci. 5:87-90.

Gorz, H. J., F. A. Haskins, and K. P. Vogel. 1982. Divergent selection for hydrocyanic acid potential in sudangrass. Crop Sci. 22:322-325.

Hakim, R. M., J. C. Sentz, and V. R. Carangal. 1969. Mass and family selection for yield in a tropical variety of maize. Agron. Abstr., p. 7.

Hallauer, A. R. 1968. Effect of mass selection for divergent ear length on yield in maize. Agron. Abstr., p. 9.

Hallauer, A. R., and J. B. Miranda. 1981. Quantitative genetics in maize breeding. Iowa State University Press, Ames, Iowa.

Hallauer, A. R., and J. H. Sears. 1969. Mass selection for yield in two varieties of maize. Crop Sci. 9:47-50.

Hallauer, A. R., and J. H. Sears. 1972. Integrating exotic germplasm into corn belt maize breeding programs. Crop Sci. 12:203-206.

Hallauer, A. R., and J. A. Wright. 1967. Genetic variance in the open pollinated variety of maize Iowa Ideal. Der Züchter 37:178-185.

Hallauer, A. R., L. Pollak, W. A. Russell, O. S. Smith, and N. Vakili. 1982. Annual report of corn breeding investigations. Iowa State University, Ames, Iowa.

Hallauer, A. R., L. Pollak, W. A. Russell, O. S. Smith, and N. Vakili. 1983. Annual report of corn breeding investigations. Iowa State University, Ames, Iowa.

Hammond, J. J., and C. O. Gardner. 1974. Modifications of the variety cross diallel model for evaluating cycles of selection. Crop Sci. 14:6-8.

Hanson, W. D. 1973. Changes in efficiencies and number of chloroplasts associated with divergent selection for juvenile productivity in Zea mays L. Crop Sci. 13:334-339.

Hooper, A. C. B. 1977. Effects of divergent selection for body weight on bone length and diameter in mice. Animal Production 24:77-82.

Johnson, E. C. 1963. Mass selection for yield in a tropical corn variety. Am. Soc. Agron. Abstr., p. 82.

Josephson, L. M., H. C. Kincer, and B. G. Harville. 1976. Selection studies for low ear placement in corn. Proc. Ann. Corn Sorghum Res. Conf. 31:85-97.

Kincer, H. C., and L. M. Josephson. 1976. Mass selection for prolificacy in corn. Agron. Abstr., p. 55.

Lantin, M. M. 1980. Observed response and genetic variability in two maize populations after four cycles of reciprocal full-sib selection. Ph.D. dissertation. Iowa State University, Ames, Iowa.

Lindsey, M. F. 1957. Genetic variance estimates in three corn belt varieties of corn. M.S. Thesis. University of Nebraska, Lincoln, Nebraska.

Lonnquist, J. H. 1952. Recurrent selection. Ann. Ind. Res. Conf. 7: 20-32.

Lonnquist, J. H. 1967. Mass selection for prolificacy in maize. Der Züchter 37:185-188.

Lonnquist, J. H., and D. P. McGill. 1956. Performance of corn synthetics in advanced generation of synthesis and after two cycles of recurrent selection. Agron. J. 48:249-253.

Mareck, J. H., and C. O. Gardner. 1979. Response to mass selection in maize and stability of resulting populations. Crop Sci. 19:779-783.

Martin, M. J. 1982. Agronomic evaluation of a maize synthetic after three cycles of recurrent selection for improved stalk quality. Ph.D. dissertation. Iowa State University, Ames, Iowa.

Martin, M. J., and W. A. Russell. 1984. Response of a maize synthetic to recurrent selection for stalk quality. Crop Sci. 24:331-337.

Mathema, B. B. 1971. Evaluation of progress in adapted x exotic maize population undergoing adaptive mass selection in Nebraska. M.S. thesis. University of Nebraska, Lincoln, Nebraska.

Mather, K. 1949. Biometrical genetics. Methuen, London.

Mode, C. J., and H. F. Robinson. 1959. Pleiotropism and the genetic variance and covariance. Biometrics 15:518-537.

Mulamba, N. N. 1981. Evaluation of mass selection for grain yield and estimation of genetic variability in three selected maize (Zea mays L.) populations. Ph.D. dissertation. Iowa State University, Ames, Iowa.

Mulamba, N. N., A. R. Hallauer, and O. S. Smith. 1983. Recurrent selection for grain yield in a maize population. Crop Sci. 23:536-540.

Nestor, K. E., W. L. Bacon, and A. L. Lambio. 1983. Divergent selection for egg production in Coturnix coturnix japonica. Poultry Sci. 62: 1548-1552.

Obilana, T. 1974. Mass selection for yield and earliness in a Nigerian maize composite. Abstr. Ann. Conf. Genet. Soc., Nigeria.

Padgett, C. H., W. A. Compton, and J. H. Lonnquist. 1968. Divergent mass selection in corn for seed size. Agron. Abstr., p. 16.

Reeve, E. C. R., and F. W. Robertson. 1953. Studies in quantitative inheritance. II. An analysis of a strain of Drosophila melanogaster selected for long wings. J. Genet. 51:276-316.

Robinson, H. F., R. E. Comstock, and P. Harvey. 1949a. Estimates of heritability and the degree of dominance in corn. Agron. J. 41: 353-359.

Robinson, H. F., R. E. Comstock, and P. Harvey. 1949b. Genetic variation in open pollinated varieties of corn. Genetics 40:45-60.

Ross, W. M., J. W. Maranville, G. Hookstra, and K. D. Kofoid. 1985. Divergent mass selection for grain protein in sorghum. Crop Sci. 25:279-282.

Russell, W. A., L. H. Penny, A. R. Hallauer, S. A. Eberhart, G. E. Scott, W. D. Guthrie, and F. F. Dicke. 1971. Registration of maize germplasm synthetics. Crop Sci. 11:140-141.

Satterthwaite, F. E. 1946. An approximate distribution of estimates of variance components. Biom. Bull. 2:110-114.

Searle, S. R. 1965. The value of indirect selection. I. Mass selection. Biometrics 21:682-707.

Smith, L. H. 1909. The effect of selection upon certain characters in the corn plant. Illinois Agric. Exp. Sta. Bull. No. 137:47-62.

Smith, O. S. 1979a. A model for evaluating progress from recurrent selection. Crop Sci. 19:223-226.

Smith, O. S. 1979b. Application of a modified diallel analysis to evaluate recurrent selection for grain yield in maize. Crop Sci. 19:819-822.

Sprague, G. F. 1966. Quantitative genetics in plant improvement. In K. F. Frey (ed.) Plant breeding. Iowa State University Press, Ames, Iowa.

Torregroza, M. 1973. Response of a highland maize synthetic to eleven cycles of divergent mass selection for ears per plant. Agron. Abstr., p. 20.

Torregroza, M., and D. D. Harpstead. 1967. Effects of mass selection for ears per plant in maize. Agron. Abstr., p. 20.

Troyer, A. F., and W. L. Brown. 1972. Selection for early flowering in corn. Crop Sci. 12:301-304.

Troyer, A. F., and W. L. Brown. 1976. Selection for early flowering in corn. Crop Sci. 16:767-772.

Tseng, C. T., W. D. Guthrie, W. A. Russell, J. C. Robbins, J. R. Coats, and J. J. Tollefson. 1984. Evaluation of two procedures to select for resistance to the European corn borer in a synthetic cultivar of maize. Crop Sci. 24:1129-1133.

Vera, G. A., and P. L. Crane. 1970. Effects of selection for lower ear height in synthetic populations of maize. Crop Sci. 10:286-288.

Vogel, K. P., F. A. Haskins, and H. J. Gorz. 1981. Divergent selection for in vitro dry matter digestibility in switchgrass. Crop Sci. 21:39-41.

Wessel-Beaver, L., R. J. Lambert, and J. W. Dudley. 1985. Genetic variability and correlations in a modified endosperm texture opaque-2 maize populations. Crop Sci. 25:129-132.

Williams, C. G., and F. A. Welton. 1915. Corn experiments. Ohio Agric. Exp. Sta. Bull. 282.

Zuber, M. S., M. L. Fairchild, A. J. Keaster, V. L. Fergason, G. F. Krause, E. Hilderbrand, and P. Loesch, Jr. 1971. Evaluation of ten generations of mass selection for corn earworm resistance. Crop Sci. 11:16-18.

ACKNOWLEDGMENTS

I wish to thank my home agency, the Institute of Plant Breeding, for granting me the precious opportunity of studying here at Iowa State University for my Ph.D.

I would like also to express my profound gratitude to Dr. A. R. Hallauer for serving as my major professor and for his help in the conduct and writing of my dissertation. His expertise in plant breeding and human relations and attitude towards field work have been truly educational for me.

The willingness of Drs. W. A. Russell, I. T. Carlson, I. C. Anderson, and C. R. Stewart to serve in my graduate committee is also sincerely appreciated.

To Jim Sears, Bill Akins, fellow corn breeding graduate students and other members of the corn breeding crew: thanks a lot for all the help during the conduct of my experiments.

I wish also to thank Sue Bennett for letting me avail of her typing skill so that all the ideas in my thesis could be read in respectable print.

Thanks, of course, to my family and friends back home and here for the moral support they have given. Special thanks are due to my parents for their constant encouragements and prayers. Thanks are also due to the Filipino community at Ames for being my second (big) family during my stay here.

And finally, thanks to God for everything.

APPENDIX

Table A1. Analysis of variance for six agronomic traits of the original and derived subpopulations of BSLE and checks grown at Location A in Ames, Iowa, in 1982

Source of variation	Degrees of freedom	Mean squares					
		Yield	Stand	Root lodging	Stalk lodging	Dropped ears	Moisture
Replication	2	86.29	21.24	795.66	1.88	0.68	1.71
Population	29	278.65**	13.75^{ns}	805.81**	129.06**	1.90^{ns}	5.06^{ns}
Error	58	43.78	16.93	207.22	31.60	2.95	3.11
Total	89						
Mean		37.39 q ha^{-1}	44.4	26.46%	11.76%	0.98%	28.42%
CV (%)		17.70	9.27	54.39	47.81	174.94	6.21

**Indicates significance at 0.01 probability level.

^{ns}Indicates nonsignificance.

Table A2. Analysis of variance for ear length and 13 other traits of the original and derived populations of BSLE and checks grown at Location B in Ames, Iowa, in 1982

Source of variation	Degrees of freedom	Ear length	Yield	Ear diameter	Cob diameter	Kernel depth	Kernel rows
Replication	2	3.82	3.58	0.03	0.02	0.002	0.64
Population	29	31.81**	132.84**	0.20**	0.03**	0.040**	4.18*
Error	58	0.91	27.90	0.02	0.01	0.005	0.64
Total	69						
Mean		21.40 cm	53.0q ha^{-1}	4.72 cm	3.05 cm	0.83 cm	16.40
CV (%)		4.45	9.97	3.28	2.79	8.36	4.86

*,** Indicate significance at 0.01 and 0.05 probability levels, respectively.

ns Indicates nonsignificance.

Mean squares							
Ears plant^{-1}	Stand	Root lodging	Stalk lodging	Dropped ears	Silking date	Plant height	Ear height
0.02	0.24	54.68	96.51	36.40	55.48	36.81	92.81
0.01^{ns}	0.88^{ns}	38.29^{ns}	408.98*	14.63^{ns}	24.75**	1751.56**	802.38**
0.01	1.07	23.99	148.00	11.40	3.34	93.05	62.76
1.04	25.23	4.15%	30.94%	2.97%	30.46days	252.02cm	127.99cm
8.68	4.10	118.00	39.31	113.82	6.00	3.83	6.19

Table A3. Analysis of variance for six agronomic traits of the original and derived subpopulations of BSLE and checks grown at Ankeny, Iowa, in 1982

Source of variation	Degrees of freedom	Mean squares					
		Yield	Stand	Root lodging	Stalk lodging	Dropped ears	Moisture
Replication	2	30.17	13.34	35.07	0.65	35.06	0.31
Population	29	792.09**	13.60*	71.98**	105.70**	6.60^{ns}	2.90^{ns}
Error	68	140.19	8.17	25.77	34.14	4.79	1.92
Total	89						
Mean		50.43 q ha^{-1}	46.38	6.79%	20.31%	1.64%	20.95%
CV (%)		23.48	6.16	74.72	28.88	133.68	6.62

*,** Indicate significance at 0.01 and 0.05 probability levels, respectively.

ns Indicates nonsignificance.

Table A4. Analysis of variance for six agronomic traits of the original and derived populations of BSLE and checks grown at Martinsburg, Iowa, in 1982

Source of variation	Degrees of freedom	Mean squares					
		Yield	Stand	Root lodging	Stalk lodging	Dropped ears	Moisture
Replication	2	313.75	3.34	139.52	3084.22	0.35	2.56
Population	29	320.88**	7.54^{ns}	16.21^{ns}	609.62**	12.52*	0.77^{ns}
Error	58	46.32	6.77	20.42	192.51	7.21	0.98
Total	89						
Mean		31.67 q ha^{-1}	48.10	3.48%	44.59%	2.68%	18.92%
CV (%)		21.49	5.41	129.99	31.11	100.01	5.24

*,** Indicate significance at 0.01 and 0.05 probability levels, respectively.

^{ns}Indicates nonsignificance.

Table A5. Analysis of variance for six agronomic traits of the original and derived subpopulations of BSLE and checks grown at location A in Ames, Iowa, in 1983

Source of variation	Degrees of freedom	Mean squares					
		Yield	Stand	Root lodging	Stalk lodging	Dropped ears	Moisture
Replication	2	27.32	33.88	1.92	148.34	18.59	1.82
Population	29	242.58**	11.40^{ns}	74.04**	127.33**	6.07^{ns}	2.62*
Error	58	35.60	8.36	27.53	48.76	4.27	1.44
Total	89						
Mean		24.86 q ha^{-1}	46.86	8.50%	20.54%	1.65%	21.46%
CV (%)		22.94	6.17	61.70	34.00	125.35	5.59

*,** Indicate significance at 0.05 and 0.01 probability levels, respectively.

^{ns}Indicates nonsignificance.

Table A6. Analysis of variance for ear length and 12 other traits of original and derived populations of BSLE and checks grown at Location B in Ames, Iowa, in 1983

Source of variation	Degrees of freedom	Ear length	Yield	Ear diameter	Cob diameter	Kernel depth	Kernel rows
Replication	2	3.54	14.08	0.07	0.01	0.01	0.29
Population	29	38.39**	492.36**	0.10**	0.02*	0.02**	3.32**
Error	58	31.55	31.55	0.02	0.01	0.01	0.87
Total	89						
Mean		37.31 cm	37.31q ha^{-1}	4.15 cm	2.77 cm	0.69 cm	15.74cm
CV (%)		15.05	15.05	3.82	3.76	10.29	5.94

*,** Indicate significance at 0.01 and 0.05 probability levels, respectively.

ns Indicates nonsignificance.

Mean squares						
Ears plant^{-1}	Stand	Root lodging	Stalk lodging	Silking date	Plant height	Ear height
0.003	27.90	405.80	19.70	4.48	764.94	283.91
0.039**	16.26^{ns}	77.46*	57.86^{ns}	18.96**	1390.17**	523.22**
0.011	18.35	46.54	37.38	3.42	122.04	52.31
0.72	45.93	10.72%	12.92%	33.31 days	233.37 cm	117.09 cm
14.68	9.32	63.64	47.30	5.55	4.74	6.18

Table A7. Analysis of variance for eight agronomic traits of the original and derived subpopulations of BSLE and checks grown at Ankeny, Iowa, in 1983

Source of variation	Degrees of freedom	Mean squares							
		Ear length	Yield	Ear diameter	Cob diameter	Kernel depth	Kernel rows	Ears plant^{-1}	Stand
Replication	2	0.94	242.17	0.007	0.003	0.001	0.12	0.09	24.44
Population	29	25.01**	276.31**	0.028^{ns}	0.014*	0.009^{ns}	2.00**	0.03**	19.15^{ns}
Error	58	2.08	15.50	0.033	0.007	0.007	0.59	0.01	16.06
Total	89								
Mean		18.52 cm	25.11a ha^{-1}	3.91	2.67 cm	0.62 cm	15.11	0.66	43.10
CV (%)		7.80	15.68	4.63	3.16	13.21	5.10	14.11	9.30

*,** Indicate significance at 0.05 and 0.01 probability levels, respectively.

ns Indicates nonsignificance.

Table A8. Observed (O) and estimated (E) ear length means (cm) with the estimated response (b) and the ratio (R) of linear regression to the total observed variation for the original and derived populations of Iowa Long Ear Synthetic

Cycle (i)	Short (Si)		Long (Li)		Original x Si		Original x Li		Si x Li	
	O	E	O	E	O	E	O	E	O	E
0	20.02	20.04	20.02	20.04	20.02	20.02	20.02	20.02	20.02	19.94
3	17.55	18.67	21.77	21.18	18.88	19.47	19.98	20.45	20.30	20.11
6	18.00	17.30	22.68	22.32	20.00	18.92	21.27	20.88	20.41	20.28
9	15.56	15.94	23.64	23.46	18.11	18.37	21.18	21.31	19.89	20.44
12	14.27	14.57	24.37	24.60	17.72	17.82	22.51	21.73	20.18	20.61
15	13.62	13.20	25.56	25.74	17.20	17.27	21.56	22.16	21.36	20.77
b(unit cycle^{-1})	0.46±0.003		0.38±0.03		-0.18±0.04		0.14±0.04		0.06±0.04	
b(% cycle^{-1})	2.30		1.90		-0.90		0.70		0.30	
R (%)	82.56				36.09				2.44	

Table A9. Observed (O) and estimated (E) yield means (q ha^{-1}) with the estimated response (b) and the ratio (R) of linear regression to the total observed variation for the original and derived populations of Iowa Long Ear Synthetic

Cycle (i)	Short (Si)		Long (Li)		Original x Si		Original x Li		Si x Li	
	O	E	O	E	O	E	O	E	O	E
0	37.48	39.47	37.48	39.47	37.48	37.69	37.48	37.69	37.48	37.97
3	36.44	36.36	38.39	38.15	38.47	37.22	37.09	37.62	37.40	37.30
6	32.04	33.26	40.20	36.82	35.42	36.76	37.61	37.54	37.55	36.63
9	32.84	30.15	33.25	35.50	36.70	36.28	38.34	37.47	34.91	35.97
12	26.53	27.04	35.95	34.17	34.84	35.82	37.75	37.39	36.69	35.30
15	23.19	23.93	31.36	32.84	36.16	35.35	36.59	37.32	33.76	34.63
b(units $cycle^{-1}$)	-1.04±0.11		-0.44±0.11		-0.16±0.11		-0.02±0.11		-0.02±0.12	
b(% $cycle^{-1}$)	-2.63		-1.11		-0.42		-0.05		-0.05	
R(%)	11.56				0.32				0.74	

Table A10. Observed (O) and expected (E) ear diameter means (cm) with the estimated response (b) and the ratio (R) of linear regression to the total observed variation for the original and derived populations of Iowa Long Ear Synthetic

Cycle (i)	Short (Si)		Long (Li)		Original x Si		Original x Li		Si x Li	
	O	E	O	E	O	E	O	E	O	E
0	4.233	4.239	4.233	4.239	4.233	4.208	4.233	4.208	4.233	4.281
3	4.256	4.302	4.222	4.187	4.256	4.242	4.200	4.187	4.244	4.286
6	4.422	4.365	4.156	4.134	4.267	4.275	4.100	4.166	4.389	4.292
9	4.444	4.428	3.900	4.082	4.278	4.309	4.167	4.145	4.367	4.297
12	4.556	4.490	4.133	4.030	4.322	4.342	4.156	4.124	4.278	4.302
15	4.478	4.553	3.989	3.978	4.411	4.375	4.089	4.103	4.256	4.308
b(units cycle^{-1})	0.021±0.004		-0.017±0.004		0.011±0.003		-0.007±0.003		0.002±0.005	
b(% cycle^{-1})	0.49		-0.40		0.26		-0.17		0.05	
R (%)	19.05				5.32				0.005	

Table A11. Observed (O) and expected (E) cob diameter means (cm) with the estimated response (b) and the ratio (R) of linear regression to the total observed variation for the original and derived populations of Iowa Long Ear Synthetic

Cycle (i)	Short (Si)		Long (Li)		Original x Si		Original x Li		Si x Li	
	O	E	O	E	O	E	O	E	O	E
0	2.811	2.812	2.811	2.812	2.811	2.834	2.811	2.834	2.811	2.828
3	2.822	2.832	2.833	2.818	2.867	2.836	2.811	2.830	2.822	2.839
6	2.878	2.852	2.811	2.824	2.889	2.839	2.800	2.826	2.867	2.850
9	2.856	2.872	2.767	2.830	2.811	2.841	2.822	2.823	2.922	2.861
12	2.978	2.892	2.856	2.836	2.878	2.844	2.844	2.819	2.856	2.872
15	2.844	2.912	2.867	2.842	2.811	2.846	2.811	2.816	2.856	2.882
b(units cycle^{-1})	0.007±0.002		0.002±0.002		0.001±0.002		-0.001±0.002		0.004±0.003	
b(% cycle^{-1})	0.25		0.07		0.04		-0.04		0.14	
R (%)	2.51				0.23				1.05	

Table A12. Observed (O) and expected (E) kernel depth means (cm) with the estimated response (b) and the ratio (R) of linear regression to the total observed variation for the original and derived populations of Iowa Long Ear Synthetic

Cycle (i)	Short (Si)		Long (Li)		Original x Si		Original x Li		Si x Li	
	O	E	O	E	O	E	O	E	O	E
0	0.706	0.712	0.706	0.712	0.706	0.685	0.706	0.685	0.706	0.723
3	0.717	0.734	0.694	0.684	0.694	0.701	0.694	0.677	0.711	0.721
6	0.772	0.756	0.672	0.656	0.689	0.717	0.650	0.669	0.761	0.719
9	0.794	0.778	0.578	0.628	0.733	0.733	0.672	0.661	0.722	0.718
12	0.789	0.799	0.639	0.599	0.722	0.749	0.656	0.652	0.711	0.716
15	0.817	0.821	0.561	0.571	0.800	0.765	0.638	0.644	0.700	0.714
b(units cycle^{-1})	0.007±0.002		-0.009±0.002		0.005±0.001		-0.003±0.001		-0.001±0.002	
b(% cycle^{-1})	0.98		-1.26		0.73		-0.44		-0.14	
R (%)	32.42				13.06				0.06	

Table A13. Observed (O) and expected (E) mean number of kernel rows with the estimated response (b) and the ratio (R) of linear regression to the total observed variation for the original and derived populations of Iowa Long Ear Synthetic

Cycle (i)	Short (Si)		Long (Li)		Original x Si		Original x Li		Si x Li	
	O	E	O	E	O	E	O	E	O	E
0	15.91	15.63	15.91	15.63	15.91	15.40	15.91	15.40	15.91	15.86
3	15.53	16.08	15.20	15.40	15.76	15.60	14.91	15.30	15.38	15.86
6	16.82	16.53	15.40	15.17	15.24	15.80	15.24	15.19	16.18	15.86
9	17.16	16.97	14.45	14.94	15.82	16.00	14.96	15.08	16.04	15.86
12	17.59	17.42	15.02	14.71	16.58	16.19	15.09	14.98	16.22	15.86
15	17.62	17.87	14.44	14.48	16.38	16.39	14.91	14.87	15.42	15.86
b(units cycle^{-1})	0.15±0.02		-0.08±0.02		0.06±0.02		-0.04±0.02		-0.0004±0.0225	
b(% cycle^{-1})	0.96		-0.51		0.39		-0.26		-0.002	
R (%)	56.51				20.01				0.0004	

Table A14. Observed (O) and expected (E) ears per plant means with the estimated response (b) and the ratio (R) of linear regression to the total observed variation for the original and derived populations of Iowa Long Ear Synthetic

Cycle (i)	Short (Si)		Long (Li)		Original x Si		Original x Li		Si x Li	
	O	E	O	E	O	E	O	E	O	E
0	0.791	0.827	0.791	0.827	0.791	0.794	0.791	0.794	0.791	0.800
3	0.842	0.807	0.819	0.822	0.808	0.789	0.810	0.798	0.832	0.797
6	0.747	0.787	0.866	0.817	0.769	0.785	0.773	0.803	0.766	0.796
9	0.790	0.766	0.791	0.812	0.762	0.780	0.821	0.807	0.783	0.793
12	0.728	0.746	0.847	0.807	0.786	0.775	0.837	0.811	0.810	0.791
15	0.735	0.726	0.764	0.802	0.775	0.798	0.796	0.815	0.784	0.788
b(units cycle^{-1})	-0.007±0.002		-0.002±0.002		-0.002±0.002		0.001±0.002		-0.001±0.002	
b(% cycle^{-1})	-0.85		-0.24		-0.25		0.12		-0.12	
R (%)	1.97				0.53				0.05	

Table A15. Observed (O) and expected (E) stand count means with the estimated response (b) and the ratio (R) of linear regression to the total observed variation for the original and derived populations of Iowa Long Ear Synthetic

Cycle (i)	Short (Si)		Long (Li)		Original x Si		Original x Li		Si x Li	
	O	E	O	E	O	E	O	E	O	E
0	43.00	42.98	43.00	42.98	43.00	42.64	43.00	92.64	43.00	42.90
3	43.38	43.21	42.28	42.81	42.33	42.86	43.67	42.71	42.71	42.85
6	44.09	43.45	41.05	42.63	92.86	43.08	42.95	42.78	42.90	42.79
9	44.38	43.68	43.19	42.45	42.67	43.30	41.52	42.85	42.57	42.73
12	44.86	43.91	42.57	42.27	43.81	43.52	43.28	42.92	42.71	42.68
15	42.67	44.14	42.14	42.09	44.10	43.74	43.24	42.99	42.67	42.62
b(units cycle^{-1})	0.08±0.05		-0.06±0.05		0.07±0.06		0.02±0.06		-0.02±0.05	
b(% cycle^{-1})	0.19		-0.14		0.16		0.05		-0.05	
R (%)	0.65				0.16				0.01	

Table A16. Observed (O) and expected (E) root lodging means (%) with the estimated response (b) and the ratio (R) of linear regression to the total observed variation for the original and derived populations of Iowa Long Ear Synthetic

Cycle (i)	Short (Si)		Long (Li)		Original x Si		Original x Li		Si x Li	
	O	E	O	E	O	E	O	E	O	E
0	10.74	11.29	10.74	11.29	10.74	12.04	10.74	12.04	10.74	10.41
3	7.69	9.40	15.33	12.55	11.09	10.66	12.41	12.89	9.14	9.67
6	3.22	7.51	14.32	13.81	11.16	9.28	14.62	13.75	8.31	8.93
9	8.27	5.63	17.06	15.06	7.24	7.89	16.14	14.61	9.50	8.19
12	2.70	3.74	17.88	16.32	3.67	6.52	14.97	15.47	7.13	7.45
15	3.16	1.85	14.38	17.58	6.96	5.14	15.55	16.32	6.53	6.71
b(units cycle^{-1})	-0.63±0.13		0.42±0.13		-0.46±0.13		0.28±0.13		-0.25±0.13	
b(% cycle^{-1})	-5.58		3.72		-3.82		2.32		-2.40	
R (%)	12.63				8.15				1.85	

Table A17. Observed (O) and expected (E) stalk lodging means (%) with the estimated response (b) and the ratio (R) of linear regression to the total observed variation for the original and derived populations of Iowa Long Ear Synthetic

Cycle (i)	Short (Si)		Long (Li)		Original x Si		Original x Li		Si x Li	
	O	E	O	E	O	E	O	E	O	E
0	32.29	30.26	32.29	30.26	32.29	29.08	32.29	29.08	32.29	31.40
3	27.14	26.34	27.31	29.86	23.76	27.32	31.77	28.53	26.05	29.31
6	22.82	22.48	29.14	29.46	27.18	25.56	25.62	27.99	27.71	27.21
9	16.41	18.59	30.75	29.06	22.06	23.80	23.32	27.44	26.41	25.12
12	12.42	14.71	28.83	28.67	22.24	22.04	25.90	26.90	27.54	23.02
15	13.67	10.82	27.76	28.27	21.23	20.28	29.93	26.35	16.99	20.93
b(units cycle^{-1})	-1.30±0.17		-0.13±0.17		-0.59±0.15		-0.18±0.15		-0.70±0.18	
b(% cycle^{-1})	-4.30		-0.43		-2.03		-0.62		-2.23	
R(%)	13.48				2.64				4.49	

Table A18. Observed (O) and expected (E) means of ear droppage (%) with the estimated response (b) and the ratio (R) of linear regression to the total observed variation for the original and derived populations of Iowa Long Ear Synthetic

Cycle (i)	Short (Si)		Long (Li)		Original x Si		Original x Li		Si x Li	
	O	E	O	E	O	E	O	E	O	E
0	2.36	2.19	2.36	2.19	2.36	1.99	2.36	1.99	2.36	3.44
3	1.58	1.73	2.43	2.32	1.82	2.05	1.63	2.11	4.33	3.18
6	0.90	1.27	2.85	2.44	1.66	2.12	2.84	2.24	2.84	2.91
9	0.53	0.81	2.20	2.57	2.29	2.18	2.44	2.36	3.33	2.64
12	0.29	0.35	3.34	2.69	2.45	2.24	2.47	2.48	2.01	2.38
15	0.30	0.11	2.33	2.82	2.31	2.31	2.42	2.61	1.79	2.11
b(units cycle^{-1})	-0.15±0.04		0.04±0.04		0.02±0.05		0.04±0.05		-0.09±0.06	
b(% cycle^{-1})										
R (%)	13.93				0.38				2.14	

Table A19. Observed (O) and expected (E) mean grain moisture content (%) with the estimated response (b) and the ratio (R) of linear regression to the total observed variation for the original and derived populations of Iowa Long Ear Synthetic

Cycle (i)	Short (Si)		Long (Li)		Original x Si		Original x Li		Si x Li	
	O	E	O	E	O	E	O	E	O	E
0	21.98	21.94	21.98	21.94	21.98	22.08	21.98	22.08	21.98	22.04
3	22.33	22.15	22.40	22.24	21.92	22.10	22.15	22.13	22.12	22.18
6	22.48	22.36	21.61	22.54	22.60	22.12	22.02	22.19	22.28	22.33
9	22.98	22.57	23.01	22.85	21.52	22.14	22.58	22.24	22.92	22.48
12	22.68	22.78	22.96	23.15	22.63	22.16	22.61	22.30	22.47	22.63
15	22.75	22.99	23.86	23.46	22.02	22.18	21.96	22.35	22.68	22.77
b(units cycle^{-1})	0.07±0.02		0.10±0.02		0.01±0.03		0.02±0.03		0.05±0.03	
b(% cycle^{-1})	0.32		0.46		0.04		0.09		0.23	
R (%)	1.15				0.04				0.43	

Table A20. Observed (O) and expected (E) mean silking date[a] with the estimated response (b) and the ratio (R) of linear regression to the total observed variation for the original and derived populations of Iowa Long Ear Synthetic

Cycle (i)	Short (Si)		Long (Li)		Original x Si		Original x Li		Si x Li	
	O	E	O	E	O	E	O	E	O	E
0	30.83	31.80	30.83	31.80	30.83	32.02	30.83	32.02	30.83	32.38
3	30.33	31.01	34.17	32.78	31.33	31.69	32.67	32.30	33.83	33.33
6	30.33	30.22	34.17	33.76	31.67	31.36	33.50	32.58	32.67	32.28
9	27.83	29.43	36.00	34.74	31.00	31.03	33.67	32.87	32.50	32.22
12	30.17	28.64	35.33	35.73	31.33	30.70	33.17	33.15	32.17	32.17
15	27.67	27.84	35.83	36.71	29.83	30.37	32.50	33.43	31.50	32.12
b(units cycle^{-1})	-0.26±0.06		0.33±0.06		-0.11±0.04		0.09±0.04		-0.02±0.05	
b(% cycle^{-1})	-0.82		1.04		-0.34		0.28		-0.06	
R (%)	47.46				15.68				0.17	

Table A21. Observed (O) and expected (E) mean plant height (cm) with the estimated response (b) and the ratio (R) of linear regression to the total observed variation for the original and derived populations of Iowa Long Ear Synthetic

Cycle (i)	Short (Si)		Long (Li)		Original x Si		Original x Li		Si x Li	
	O	E	O	E	O	E	O	E	O	E
0	238.00	241.58	238.00	241.58	238.00	250.33	238.00	250.33	238.00	247.44
3	226.67	231.90	258.83	248.76	240.50	244.65	264.67	25.388	252.67	246.48
6	214.83	222.21	256.83	255.94	246.17	238.97	263.83	257.43	251.00	245.53
9	212.83	212.53	275.67	263.12	232.67	233.29	261.17	260.98	247.00	244.58
12	202.00	202.85	263.50	270.29	227.50	227.61	259.83	264.53	244.83	243.63
15	197.67	193.17	273.00	277.47	220.33	221.92	267.00	268.07	236.83	242.68
b(units cycle^{-1})	-3.23±0.35		2.39±0.35		-1.89±0.29		1.18±0.29		-0.32±0.35	
b(% cycle^{-1})	-1.34		0.99		-0.76		0.47		-0.13	
R (%)	74.39				48.68				1.24	

Table A22. Observed (O) and expected (E) mean ear height (cm) with the estimated response (b) and ratio (R) of linear regression to the total observed variation for the original and derived populations of Iowa Long Ear Synthetic

Cycle (i)	Short (Si)		Long (Li)		Original x Si		Original x Li		Si x Li	
	O	E	O	E	O	E	O	E	O	E
0	118.83	122.77	118.83	122.80	118.83	125.97	118.83	125.97	118.83	124.10
3	114.00	116.35	133.33	127.82	121.50	122.84	136.83	128.35	126.83	123.65
6	107.17	109.93	132.33	132.84	120.67	119.71	131.50	130.72	125.50	124.20
9	102.83	103.50	147.83	137.86	117.83	116.58	133.17	133.10	125.00	122.75
12	96.00	97.08	142.00	142.86	113.17	113.44	135.00	135.47	124.50	122.29
15	93.50	90.66	141.67	147.88	136.83	110.31	136.17	137.84	117.17	121.84
b(units cycle^{-1})	-2.14±0.21		1.67±0.21		-1.04±0.20		0.79±0.20		-0.15±0.31	
b(% cycle^{-1})	-1.74		1.36		-0.82		0.63		-0.12	
R (%)	77.53				43.87				0.59	

Table A23. Analysis of variance for 13 traits of 300 S_1 lines of BSLE in a test conducted at Ames, 1983

Source of variation	Degrees of freedom	Mean squares				
		Ear length	Yield	Stand	Ears per plant	Plant height
Set (S)	9	15.229	403.380	16.171	0.132	5234.567
Replication/S	10	4.651	94.040	1.921	0.026	589.105
Population (P)/S	20	354.184**	486.493**	7.572*	0.103^{ns}	24144.457**
Error a	20	2.522	68.074	1.932	0.033	289.640
Entry/P/S	270	8.898**	159.772**	3.051**	0.065**	556.516**
BSLE C0	90	8.145**	141.374**	2.555*	0.065**	473.233**
BSLE C15S	90	8.465**	181.660**	2.257^{ns}	0.048**	532.456**
BSLE C15L	90	10.083**	156.281**	4.340**	0.082**	668.858**
Error b	270	2.475	41.670	1.654	0.022	173.473
BSLE C0	90	2.212	50.557	1.568	0.021	173.764
BSLE C15S	90	1.253	31.663	1.746	0.013	170.632
BSLE C15L	90	3.959	42.792	1.649	0.030	176.023
Total	599					
Mean		17.16 cm	27.19 q ha^{-1}	18.38	0.77	198.99 cm
CV (%)		9.16	23.74	7.00	19.19	6.62

*,**Indicate significance at 0.05 and 0.01 probability levels, respectively.

^{ns}Indicates nonsignificance.

Table A23. Continued

Source of variation	Degrees of freedom	Mean squares			
		Ear height	Kernel rows	Ear diameter	Cob diameter
Set (S)	9	3358.050	4.389	0.194	0.126
Replication/S	10	258.225	1.647	0.056	0.043
Population (P)/S	20	7980.435**	54.905**	1.497**	0.105*
Error a	20	203.645	0.680	0.061	0.020
Entry/P/S	270	357.438**	4.266**	0.140**	0.060**
BSLE C0	90	335.981**	4.740**	0.105**	0.056*
BSLE C15S	90	287.318**	6.011**	0.181**	0.079**
BSLE C15L	90	449.014**	2.046**	0.134*	0.062*
Error b	270	111.512	0.824	0.053	0.028
BSLE C0	90	127.538	0.660	0.042	0.034
BSLE C15S	90	87.089	1.082	0.036	0.013
BSLE C15L	90	119.909	0.732	0.082	0.038
Total	599				
Mean		92.77 cm	15.07	3.94 cm	2.75 cm
CV (%)		11.38	6.02	5.86	6.13

Table A23. Continued

Source of variation	Degrees of freedom	Mean squares			
		Kernel depth	Root lodging	Stalk lodging	Silking date
Set (S)	9	0.023	527.251	153.375	43.244
Replication/S	10	0.004	376.070	155.777	8.603
Population (P)/S	20	0.240**	1772.114**	832.692**	309.552**
Error a	20	0.012	279.215	143.634	5.548
Entry/P/S	270	0.017**	545.052**	181.482**	23.224**
BSLE C0	90	0.012*	803.448**	167.197*	24.068**
BSLE C15S	90	0.022**	247.087^{ns}	121.612**	25.834**
BSLE C15L	90	0.017^{ns}	584.630**	255.637**	19.772**
Error b	270	0.009	206.093	94.011	3.593
BSLE C0	90	0.008	267.581	115.209	4.168
BSLE C15S	90	0.007	185.182	53.735	3.298
BSLE C15L	90	0.012	167.947	113.089	3.312
Total	599				
Mean		0.595 cm	15.14%	12.84%	33.82 days
CV (%)		16.17	94.98	75.50	5.60

Table A24. Analysis of variance for 13 traits of 300 S_1 lines of BSLE in a test conducted at Ames, 1984

Source of variation	Degrees of freedom	Mean squares				
		Ear length	Yield	Stand	Ears per plant	Plant height
Set (S)	9	7.184	449.359	12.035	0.142	1422.778
Replication/S	10	9.349	95.600	9.832	0.016	442.727
Population (P)/S	20	306.642**	776.756**	11.032^{ns}	0.108**	29170.948**
Error a	20	3.104	55.640	5.342	0.017	156.492
Entry/P/S	270	6.928**	186.851**	14.545**	0.044**	752.717**
BSLE C0	90	5.592**	171.293**	9.254**	0.040**	844.669**
BSLE C15S	90	5.463**	188.426**	15.990**	0.039**	650.986**
BSLE C15L	90	9.729**	200.833**	18.391**	0.054**	762.497**
Error b	270	2.168	32.261	4.586	0.014	86.144
BSLE C0	90	1.849	37.418	3.574	0.012	89.554
BSLE C15S	90	1.004	26.200	4.897	0.011	63.339
BSLE C15L	90	3.652	23.164	5.289	0.020	105.539
Total	599					
Mean		17.45 cm	35.91 q ha^{-1}	19.63	0.85	203.64 cm
CV (%)		8.44	15.82	10.91	14.10	4.56

**Indicates significance at 0.01 probability level.

^{ns}Indicates nonsignificance.

Table A24. Continued

Source of variation	Degrees of freedom	Mean squares			
		Ear height	Kernel rows	Ear diameter	Cob diameter
Set (S)	9	492.519	2.561	0.024	0.124
Replication/S	10	93.642	0.307	0.051	0.033
Population (P)/S	20	7927.053**	47.634**	2.292**	0.182**
Error a	20	60.177	0.656	0.037	0.044
Entry/P/S	270	414.224**	5.693**	0.100**	0.065**
BSLE C0	90	473.405**	6.529**	0.120**	0.058**
BSLE C15S	90	355.378**	7.770**	0.133**	0.081^{ns}
BSLE C15L	90	413.890**	2.780**	0.108**	0.056**
Error b	270	45.691	0.768	0.031	0.033
BSLE C0	90	59.683	0.712	0.028	0.012
BSLE C15S	90	34.124	1.011	0.032	0.064
BSLE C15L	90	43.266	0.582	0.032	0.021
Total	599				
Mean		94.54 cm	16.06	4.24 cm	2.87 cm
CV (%)		7.15	5.46	4.12	6.29

Table A24. Continued

Source of variation	Degrees of freedom	Mean squares			
		Kernel depth	Root lodging	Stalk lodging	Silking date
Set (S)	9	0.023	527.251	153.375	43.244
Replication/S	10	0.004	376.070	155.777	8.603
Population (P)/S	20	0.240**	1772.114**	832.692**	309.552**
Error a	20	0.012	279.215	143.634	5.548
Entry/P/S	270	0.017**	545.052**	181.482**	23.224**
BSLE C0	90	0.012*	803.448**	167.197*	24.068**
BSLE C15S	90	0.022**	247.087^{ns}	121.612**	25.834**
BSLE C15L	90	0.017^{ns}	584.630**	255.637**	19.772**
Error b	270	0.009	206.093	94.011	3.593
BSLE C0	90	0.008	267.581	115.209	4.168
BSLE C15S	90	0.007	185.182	53.735	3.298
BSLE C15L	90	0.012	167.947	113.089	3.312
Total	599				
Mean		0.595 cm	15.14%	12.84%	33.82 days
CV (%)		16.17	94.98	75.50	5.60

*Indicates significance at 0.05 probability level.

Table A25. Analysis of variance for 10 traits of 300 S_1 lines of BSLE in a test conducted at Kanawha, 1983

Source of variation	Degrees of freedom	Mean squares				
		Ear length	Yield	Stand	Ears per plant	Plant height
Set (S)	9	15.342	397.000	3.514	0.088	492.371
Replication/S	10	6.119	177.430	3.810	0.075	341.842
Population (P)/S	20	341.321**	442.600**	2.593^{ns}	0.074	31372.83**
Error a	20	2.585	60.402	2.300	0.030	179.867
Entry/P/S	270	9.948**	184.691**	1.740^{ns}	0.062**	797.981**
BSLE C0	90	8.836**	183.117**	1.791^{ns}	0.058**	854.156**
BSLE C15S	90	8.356**	197.270**	1.765^{ns}	0.058**	879.464**
BSLE C15L	90	12.651**	173.687**	1.665^{ns}	0.070**	660.324**
Error b	270	2.062	36.685	2.048	0.026	102.447
BSLE C0	90	1.814	39.051	1.896	0.022	78.52
BSLE C15S	90	1.589	32.916	1.967	0.024	84.804
BSLE C15L	90	2.784	38.090	2.280	0.031	144.017
Total	590					
Mean		17.62 cm	28.82 q ha^{-1}	18.60	0.81	213.60 cm
CV (%)		8.15	21.02	7.70	19.80	4.74

**Indicates significance at 0.01 probability level.

^{ns}Indicates nonsignificance.

Table A25. Continued

Source of variation	Degrees of freedom	Mean squares				
		Ear height	Kernel rows	Ear diameter	Cob diameter	Kernel depth
Set (S)	9	562.663	3.420	0.179	0.121	0.036
Replication/S	10	176.332	0.344	0.116	0.022	0.025
Population (P)/S	20	11953.155**	39.370**	1.437**	0.089^{ns}	0.267**
Error a	20	102.972	0.486	0.072	0.025	0.014
Entry/P/S	270	604.555**	4.644**	0.134**	0.061**	0.019**
BSLE C0	90	723.338**	4.255**	0.114**	0.057**	0.013**
BSLE C15S	90	480.839**	6.756**	0.177**	0.066**	0.026**
BSLE C15L	90	609.485**	2.921**	0.113**	0.061**	0.017*
Error b	270	79.795	0.746	0.039	0.024	0.008
BSLE C0	90	72.001	0.532	0.023	0.021	0.007
BSLE C15S	90	30.344	0.933	0.056	0.027	0.007
BSLE C15L	90	137.042	0.773	0.037	0.025	0.011
Total	599					
Mean		96.67 cm	15.35	3.97 cm	2.80 cm	0.584 cm
CV (%)		9.24	5.63	4.97	5.54	15.65

*Indicates significance at 0.05 probability level.